REPRODUCTIVE AND LARVAL BIOLOGY OF NORTHERN SHRIMP,

PANDALUS BOREALIS KRØYER, IN RELATION TO TEMPERATURE

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REPRODUCTIVE AND LARVAL BIOLOGY OF NORTHERN SHRIMP, *PANDALUS BOREALIS* KRØYER, IN RELATION TO TEMPERATURE

A

THESIS

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ABSTRACT

The northern shrimp, Pandalus borealis Krøyer, is an important fishery resource in Alaska. However, a drastic decline in the commercial catch since 1978 poses a serious problem for the fishery. This study examined the effects of temperature on reproduction and larval survival of P. borealis. These are factors though to be vital to the determination of year class strength.

P. borealis was found to have narrow thermal requirements for egg production with moderate (6°C) to low (3°C) temperatures generally more favorable than high (9°C) temperatures. In contrast with egg production, larval survival was enhanced by higher (6 and 9°C) temperatures.

This study provides useful information for management of the fishery by demonstrating that temperature can trigger flucuations in the commercial catch from 5-50% through its effects on rates or reproduction and larval survival, and thereby population size. In warm water areas averaging >6°C, temperature exerts its main influence on reproduction, causing fecundity to vary by as much as 50%. While in colder areas average <3°C, fecundity and larval survival can vary with temperature by as much as 20 and 40%, respectively. Use of the information derived here requires monitoring temperature in the major fishery areas to detect changes in abundance of ovigerous females, egg number and larval mortality. Changes in these parameters are valuable indicators

of stock condition when combined with abundance surveys and fishing intensity estimates.

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CHAPTER 1

INTRODUCTION

A fundamental question in population dynamics is whether animal populations are in a state of long-term balance. If they are, identification of the mechanisms responsible for that balance remain largely unanswered. Many marine invertebrates and fishes exhibit widely fluctuating population sizes (Dow 1964; Blaxter and Hempel 1963; Cushing 1975). This is especially true of short-lived species and those with larval planktonic stages. Among decapod crustaceans, Pandalus borealis has a relatively short lifespan of 5-7 years with a planktonic larval period of 3-4 months. Abundance of P. borealis has fluctuated more widely than that of any other commercial species in the Gulf of Maine (Dow 1963). It has been postulated that the cyclic nature of P. borealis abundance is closely related to variation in year class success. Moreover, it is possible that fluctuations in year class recruitment may be more important than effects of fishing as the ultimate determinant of yields.

Fluctuation in abundance of P. borealis in the Gulf of Maine is believed to result primarily from physical factors (Apollonio and Dunton 1969). Seawater temperature trends associated with climatic cycles were found to be the most consistent factor influencing abundance (Dow 1979). A marked decline from 1963-1966 in the P. borealis fishery in the Skagerrak was attributed to abnormal cooling of the bottom water (Rasmussen

1967). Off Greenland, were P. borealis exists at close to the lower limits of its temperature tolerance near the northern boundary of its range, small fluctuations in temperature might have major influence on the shrimp population (Horsted and Smidt 1956, 1965). In the Bering Sea, Ivanov (1969) suggested that strong year classes resulted mainly from mild to moderate temperature conditions as indicated by the extent of ice cover. Given these observations, the main objective of this study was to investigate the effects of temperature on reproduction and larval survival of P. borealis. In the Gulf of Alaska, water temperatures vary from 1.5-12°C (Fig. 1; Table 21).

The primary hypothesis of this study is that water temperature affects reproductive output and larval survival, and thereby recruitment into the fishery four years late. In this study, adult female P. borealis were exposed to high, medium, and low temperatures to examine the hypothesis that fecundity and incubation efficiency are maximal at low temperatures. Larvae were raised at high, medium, and low temperatures to examine the hypothesis that larval survival is optimal at high temperatures. It is expected that the results of this study will effectively address the role of temperature in affecting year class recruitment.

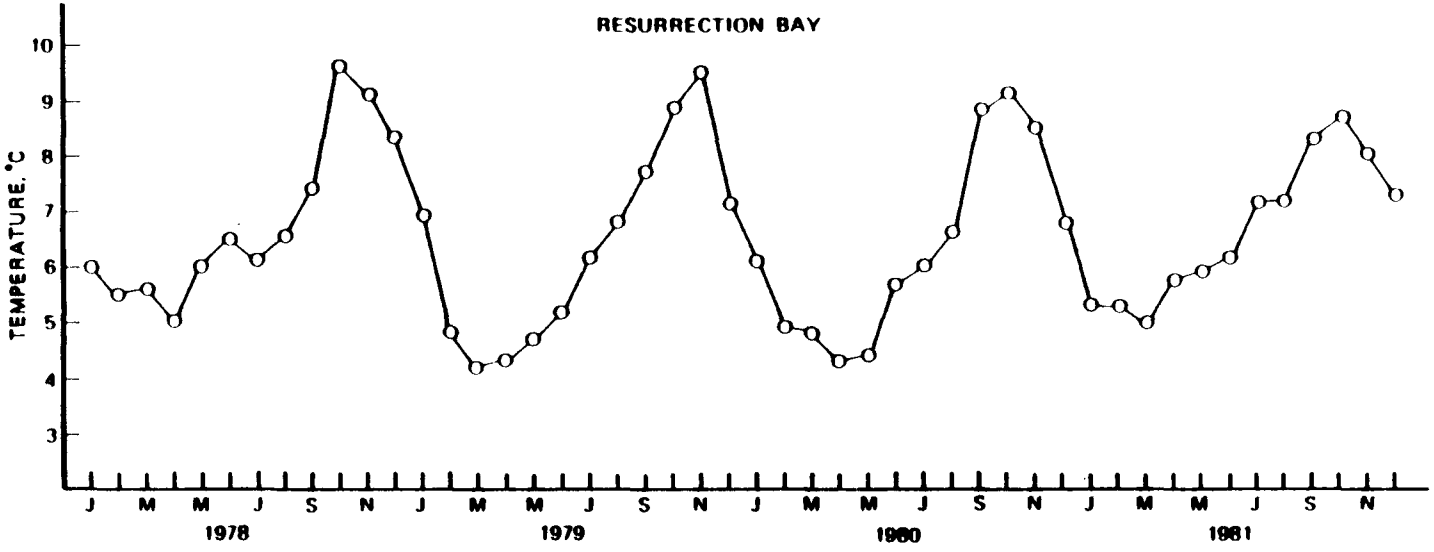


Figure 1. Mean monthly temperatures in Resurrection Bay, Gulf of Alaska from 1978-1981.

CHAPTER 2

REPRODUCTION

Oogenesis and Egg Production

Successful reproduction is basic to population dynamics. Therefore, understanding the factors influencing reproductive patterns is fundamental to an understanding of population change. Rasmussen (1953) suggested that an influx of cold water on a shrimp field over an extended period had a depressing effect on the production of new broods. Populations of P. borealis in low temperature areas in Newfoundland reproduce at low rates (Squires 1968). In warm water areas, on the other hand, P. borealis populations were found to reproduce at higher rates. Water temperature has been thought to be the factor controlling the spawning and hatching of P. borealis over its geographic range (Allen 1959; Anthony and Clark 1978; Butler 1964; Dow 1964; Haynes and Wigley 1969; Ito 1976; Ivanov 1969; Rasmussen 1953). The controlling effect of water temperature on ovarian development, however, is unresolved.

The relationship between spawning potential of the parental stock and recruitment is often obscured by fluctuations caused by environmental factors. The number of offspring of poikilothermic organisms is significantly affected by temperature and body size (Allee et. al. 1949; Grainger 1953; Steele 1964). The suggestion has been made that P. borealis is a species especially prone to natural fluctuations in abundance in relation to temperature

cycles in the sea (Apollonio and Dunton 1969; Dow 1966 a and b). These authors suggested that the effect of temperature is most apparent in the early stages of the life cycle, i.e., on the eggs. Apollonio and Dunton (1969) attributed the collapse of the P. borealis fishery in the Gulf of Maine from 1954-1957 to high winter temperatures that caused poor egg production. Forecasts of recruitment have been made based on the fecundity of the parental stock. As a reliable indicator of the reproductive potential and vigor of a population, a knowledge of fecundity is vital to those making fishery management decisions. Stickney (1980) provided evidence to show that variations in the number of eggs carried by ovigerous P. borealis were associated with subsequent fluctuations in abundance.

In this chapter, temperature effects on oogenesis and egg production in pink shrimp were examined under controlled conditions, and the results compared with natural populations.

Embryonic Development, Egg Loss and Larval Hatching Success

Pandalus borealis inhabits waters with temperatures ranging from -4 to 15°C and exhibits seasonal spawning migration that is believed to be related to cyclic changes in oceanographic conditions, particularly temperature (Butler 1972; Ivanov 1969). Annual variations and geographical differences in oceanographic conditions which prevail during the early developmental stages of P. borealis may contribute to changes in egg and larval survival, and consequently to the strength of year classes produced.

Theoretical considerations of life history patterns emphasize egg size as one of the most important aspects of reproduction (Vance 1973 a and b; Stearns 1976).

Egg size is a significant life history characteristic and is often negatively correlated with fecundity (Thorson 1950), developmental pattern (Thorson 1946, 1950), and positively with offspring size (Amio 1963; Reaka 1979). It is also the basic unit of adult reproductive energy expenditure (Menge 1975; Todd 1979). Since both the number and size of eggs produced may vary with environmental conditions, it may be important either that large numbers be produced or that eggs be provided with an optimal amount of yolk and are released under conditions favorable to their development. Therefore, it is important to determine if prevailing water temperatures during incubation influence subsequent larval viability.

The effects of temperature on egg development, loss of developing embryos, and larval hatching success were investigated in the present study. Results are compared with field data in an effort to identify environmental conditions that govern egg survival under natural conditions.

MATERIALS AND METHODS

Oogenesis and Egg Production

Sexually mature Pandalus borealis were collected from Resurrection Bay (120 m depth) aboard the commercial trawlers M/V Hasta and Tundra. The shrimp were collected in September 1979,

March 1980, October 1980, and February 1981 from the same position (60°5'N; 149°25'W). All hauls were of 30 minute duration with the same trawl used on every collection. Upon transfer to the laboratory the shrimp were held in 860 liter tanks under low light levels (50 lux) and controlled temperatures for two full reproductive cycles. The shrimp were fed ad libitum of herring, walleye pollock, halibut or mussel meat. Flow rates in the tanks were maintained at a minimum of four liters per minute. The tanks were cleaned daily of silt and other harmful elements with a tygon suction hose.

Shrimp were maintained under three temperature regimes reflecting the range of temperatures in their natural environment: low temperature (2-3°C), ambient temperature (temperature of the incoming seawater which varied seasonally from 4 to 10°C with an annual mean temperature of 6.3°C, see Appendix I, Tables 1 and 2), and high temperature (8-9°C). Low temperature was provided by Frigid Units water chillers Model D1-100. A quartz immersion heater (9000 watts) supplied water of elevated temperatures. A Yellow Springs Thermistep temperature controller Model 71-A kept water at desired temperatures.

Oogenesis - The shrimp used in reproductive studies were taken from laboratory populations maintained under low, medium, and high thermal regimes. Monthly samples of five shrimp for each 1 mm increment in carapace length from 20 to 28 mm were taken from January 1980 to December 1981 for histological

examination. These specimens represented approximately 3- to 6-year-old sexually mature females (Ivanov 1969; Butler 1972). Carapace length (CL) is the distance from the posterior edge of the eye socket to the posterior lateral edge of the carapace along the dorsal midline. Shrimp from periodic field collections were also examined. Gonadal samples, 0.1 to 1.0 cm in size, were taken at each sampling date, placed in Zenker's fixative, embedded in paraffin, sliced into 10 um thick sections, and stained with Mallory's Triple Stain.

Stages of ovarian development were classified as follows (Table 1):

Stage I-Resting or Recovering. No ovarian development visible through the carapace. The ovary beneath the exoskeleton appears as a pair of threadlike tubes joined anteriorly and medianly at the posterior end of the digestive gland. Developing oogonia and oocytes are in different stages of mitosis and meiosis. Large previtellogenic ova retained from the previous spawning period are located in peripheral areas of the germinal strand (Fig. 2).

Stage II-Intermediate or Early Active. Ovarian development covers less than 25% of the carapace length. The tubes of the ovary widen outwards to the sides of the digestive gland. Ovaries pinkish in color. Proliferation and growth of primary oocytes fill more than half the gonad, concentrating on the inner (digestive gland) side. Two large nucleoli are present in the

Table 1. Summary of characteristics of ovarian stages of maturation for Pandalus borealis.

Stage of Maturation	Microscopic Histological Description	Macroscopic Gross Appearance
I Resting/ Recovering	Small immature oocytes present in a central germinative zone or strand surrounded by larger previtellogenic ova. Developing oocytes in different stages of mitosis and meiosis.	Threadlike in two distinct tubes, resting ovaries are barely visible through the transparent carapace.
II Intermediate/ Early Active	Proliferation and growth of oocytes. Two large nucleoli present in the largest oocytes.	Growth of ovary to less than 25% of the carapace. Ovaries of pinkish red color.
III Ripening/Late Active	Yolk granules prliferating. Follicle cells surround the growing oocytes.	Dorso-ventral, lateral and anterior expansion of the ovary extending from 25 to 75% of the carapace. Ripening ovaries change from dull to bright green.
IV Ripe	Ova packed with yolk granules. No. interstitial spaces present. Vitellogenesis completed.	Greatly enlarged, intense green ripe ovaries cover greater than 75% of the carapace.
V Spent	Unspent vitellogenic ova and previtellogenic oocytes retained in peripheral areas of germinal strand. Immature oocytes present in small numbers.	Translucent, flaccid spent ovary almost invisible through the exoskeleton.

Figure 2. Ovary of Pandalus borealis in resting or recovering stage of development. A. 40X. Dividing oogonia in different stages of mitosis and meiosis. B and C. Larger previtellogenic oocytes in peripheral areas.

largest oocytes. Follicular tissue located in a narrow band around the periphery (Fig. 3).

Stage III-Ripening or Late Active. Maturing ovaries occupy between 25 to 75% of the carapace due to dorso-ventral, lateral and anterior expansion. Ripening ovaries progress from a dull to a bright green in color. Growth of oocytes continues but vitellogenesis has not begun. Follicular tissue has infiltrated around the growing oocytes and is about three cells thick. A few vacuoles are present and lipid droplets are beginning to appear (Fig. 4).

Stage IV-Ripe. With continued lateral and anterior growth, bright green ripe ovaries extend over 75% of the carapace. With vitellogenesis completed, the fully mature ovum has a chorionic membrane. Follicular cells appear in a linear arrangement around the ova. At the commencement of vitellogenesis, yolk globules localize in one hemisphere. In the mature ovum, the large yolk globules become dispersed throughout (Fig. 5).

Stage V-Spent. Greatly shrunken to two thin, flaccid strips, spent ovaries barely show through the carapace. Unspent vitellogenic ova occupy the peripheral areas of the germinal strand. Well developed follicular cells two to three layers thick surround the larger previtellogenic oocytes. Newly forming oogonia and developing primary oocytes appear in small numbers (Fig. 6).

Figure 3. Ovary of Pandalus borealis in intermediate or early active stage of maturation. A. Growth and proliferation of primary oocytes. B and C. Onset of follicular development (dark staining band surrounding clear area) around maturing previtellogenic oocytes. Two large nucleoli seen in the largest oocytes.

Figure 4. Ripening ovary of Pandalus borealis. A. Infiltration of follicular tissue. B. Oocyte in very early stages of vitellogenesis where the nucleolus is beginning to appear vacuolated. C. 40X. Yolk globules surround nucleus with a well formed membrane of a maturing ova.

Figure 5. Mature ova of Pandalus borealis. Small yolk granules surround the nucleus while larger yolk granules localize around the periphery.

Figure 6. Spent ovary of Pandalus borealis. Germinal cells and young oocytes are present in the core. Larger unspent vitellogenic ova and previtellogenic oocytes located distal to the core.

The above descriptions are divisions of convenience in a continuum as boundaries between stages are not always sharp. Proportions of shrimp in each stage were recorded and grouped by months to analyze the temporal progression of the reproductive cycle. Specimens on the borderline between two successive stages were counted as 50% in each stage.

Oocyte diameters were measured with an ocular micrometer. The oocyte diameter was taken as the greatest length in the horizontal plane. Oocyte diameters were sampled by measuring the first 100 oocytes encountered while determining proportions of oocyte types.

Four oocyte types were distinguished morphologically and are as follows:

Primary or small immature oocytes. These ranged from 20 to 40 µm in diameter and were irregular in shape. They were darkly staining and contained no yolk or fat droplets. The nucleus contained one or two small nucleoli.

Secondary or large immature oocytes. These had a more regular round shape measuring from 40 to 60 µm in diameter. The nucleus contained two large darkly staining nucleoli. They contained few fat droplets but no yolk was present.

Maturing oocytes. These were oocytes which had begun vitellogenesis and measured from 60 to 120 µm. A single large nucleolus is retained in the early stages. Large yolk globules

and lipid droplets are present. A chorionic membrane begins to form.

Atretic or regressing oocytes. Some characteristics associated with oocyte atresia are disorganization of a cellular structure including rupture of the nucleus, loss of the prominent nucleoli and reduction of follicle cells.

For each test temperature, the following data were recorded: 1) mean time for the ovarian maturation process, 2) time of appearance of first ovigerous female, 3) percent ovigerous females on first ovigerous day, 4) mean length of spawning period, and 5) maximum abundance of ovigerous females.

Egg Production - Fecundity in this study refers to the number of eggs produced by a female in one spawning season. The ovigerous shrimp used in this study were held in the laboratory under controlled temperature conditions for one full year before spawning. Egg counts were made immediately following spawning in August to October, at approximately the midpoint of embryonic development in January, and prior to hatching in February to March. Eggs were stripped from ten ovigerous females for each millimeter increment in size class from 18 to 25. Stripped eggs were placed in weak alcohol-formaldehyde-seawater solutions overnight after which they were easily separated from each other. All eggs were counted individually by hand. Egg counts of ovigerous shrimp from field collections were used as controls.

Individual egg length and width measurements were made from a representative sample of 20-40 eggs per individual. These eggs were not immersed in preservative solutions but were measured fresh immediately after being stripped off the pleopods of an egg-bearing female. Egg length and width measurements were made to the nearest 0.01 mm with a 2X objective lens and a 10X ocular micrometer. Measurements were recorded initially in ocular units and later converted to millimeters using a 100-stage micrometer and a conversion factor of 0.033 mm. Egg volumes were calculated, assuming shrimp eggs to be ellipsoid in shape.

Embryonic Development, Egg Loss and Larval Hatching Success

Ten ovigerous shrimp were exposed to each of three temperature regimes throughout the developmental period of their eggs from October 1979 to June 1982. They were held at ambient, fluctuating temperatures (mean of 5°C) to determine the developmental rates of their eggs in a regime similar to that of the natural temperature regime, and at cool (3°C) and warm temperatures (9°C).

Ovigerous shrimp were tagged to allow individual identification for sampling at two-week intervals. Twenty eggs from each tagged female were removed from the peripheral area of their egg mass during each sampling period. Continuous monitoring showed that periodic removal of eggs did not cause shedding of the remaining eggs. Identification of developmental stage and measurements of egg size were made immediately on

freshly stripped eggs. Assuming shrimp eggs to be ellipsoid in shape, egg volume was calculated using the formula:

$V=\frac{4}{3}\pi abc$, where a=egg length, b=egg width, and c=egg thickness, and assuming c=b.

Embryonic development was followed in periodically stripped eggs. Development can be divided into a series of discrete and recognizable events. This sequence of observable embryonic events appears to be similar in other decapods (Herring 1974), only the relative duration of these events proving rather variable between species. The classification scheme followed in this study was modified from that of Roberts (1975). The eggs were assigned to one of five stages. Each stage in egg development was characterized as follows:

stage 1 Blastula - nonsegmented blastoderm with undifferentiated yolk cells

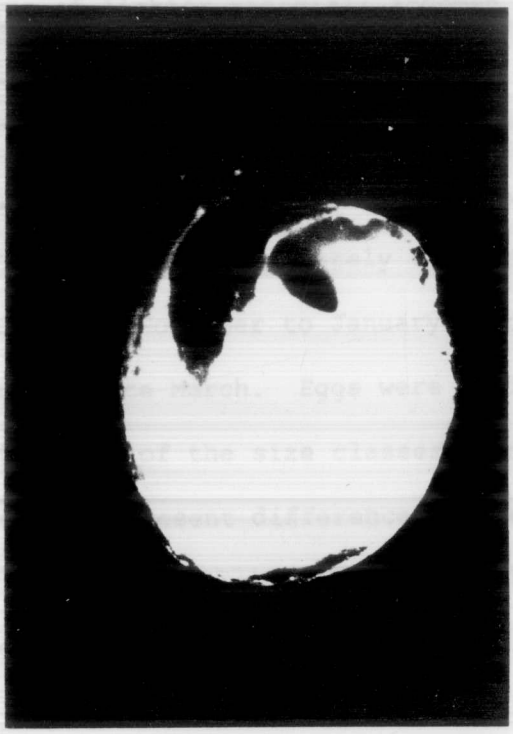
stage 2 Gastrula - yolk cells beginning to localize at one pole of the egg with the separation of embryonic from yolk tissue; early segmentation of body

stage 3 Organogenesis I - first appearance of eye pigment spot; vague outline of embryo can be seen; over one-half of the egg is yolk (Fig. 7)

stage 4 Organogenesis II - eye pigment spot becomes crescent-shaped; appendages visible; abdomen not free from head; yolk is less than one-half of the egg (Fig. 8)

Figure 7. Developing egg of Pandalus borealis in late stage 3.

Figure 8. Developing eggs of Pandalus borealis from early to late stage 4.

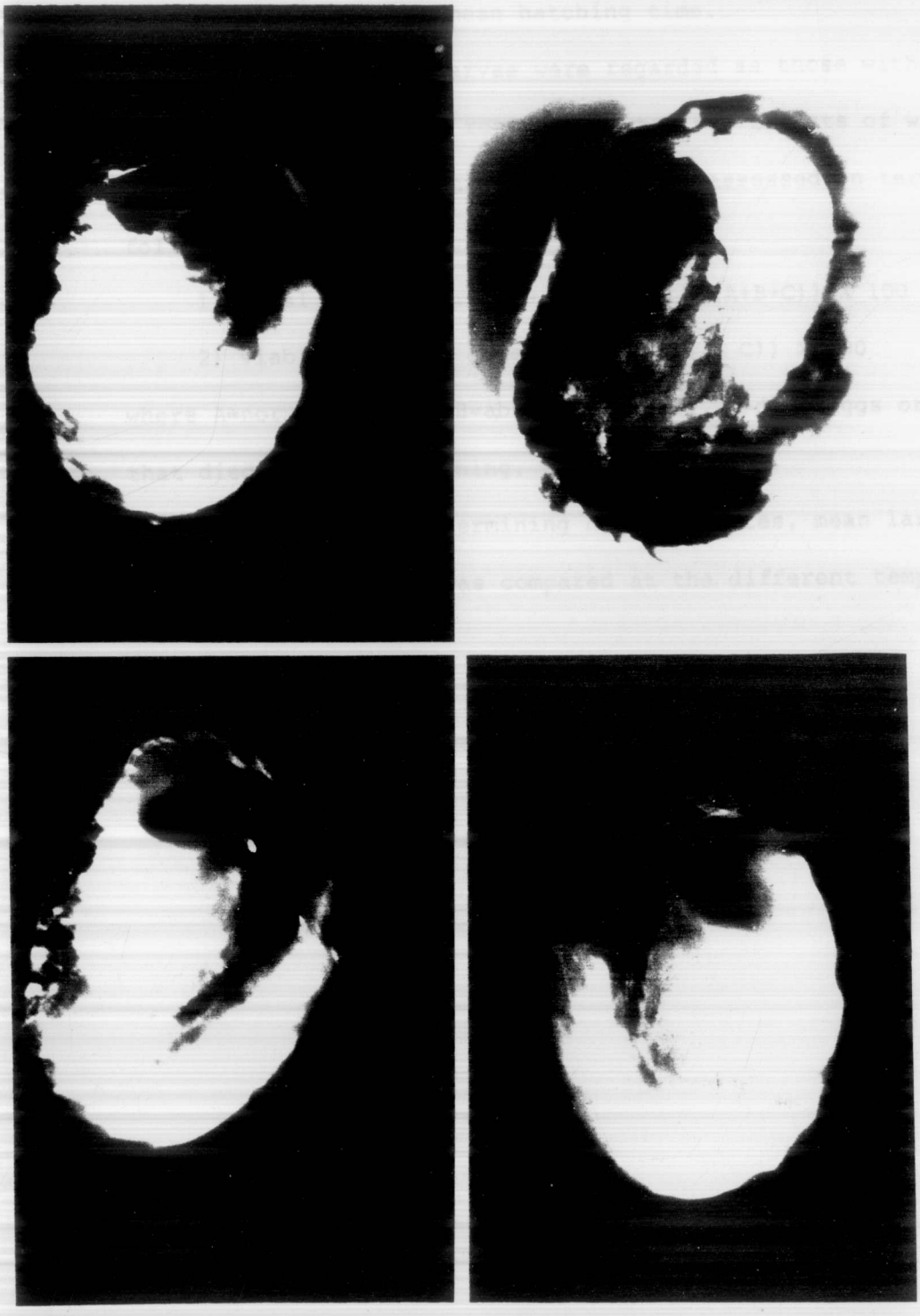


stage 5 Organogenesis III - eyes darkly pigmented with an outer ring of lighter material; abdomen free from the head; little yolk present; beating heart visible (Fig. 9).

Egg Loss - Egg counts were made immediately following spawning in August to October, at approximately the midpoint of embryonic development from mid-November to January, and prior to hatching in mid-February to late March. Eggs were stripped from ten ovigerous females for each of the size classes from 18-25 mm CL. Egg loss is given as the present difference between the mean number of eggs at spawning and the number of eggs at the midpoint and near the end of the incubation period.

Larval Hatching - Five tagged shrimp from each size class were held in separate Nalgene polyethylene animal cages partially submerged in water tanks at each of three temperatures from the time of spawning to hatching from February 1980 to June 1982. Larval hatching by individual shrimp occurred mostly in pulses over a 2-3 day period. Newly hatched larvae were collected every six hours by a wide-bore pipette. At the end of each 24-hour period, the cages were drained and the larvae collected. Subsamples of 20 newly hatched larvae from each 6-hour observation interval were measured under a dissecting microscope. Larval size (carapace length) was measured as in the adults. Mean hatching time occurred when 50% of a batch of eggs had freed themselves from the chorion. The size of larvae that hatched ±6

Figure 9. Developing eggs of Pandalus borealis from early stage 5 to hatching.



hours of mean hatching time was considered to be representative of mean larval size at mean hatching time.

Viable or normal larvae were regarded as those without damaged eyes, or broken rostrums or tails. Effects of water temperature on larval hatching rate were assessed in terms of the following formulae:

1) total hatching rate = ((A + B) / (A+B+C)) X 100

2) viable hatching rate = (A/(A + B + C)) X 100

where A=normal larvae, B=abnormal larvae, C=dead eggs or embryos that died prior to hatching.

In addition to determining hatching rates, mean larval size at mean hatching time was compared at the different temperatures.

RESULTS

Oogenesis - Based on combined data of two years, Fig. 10 illustrates the annual reproductive cycle of P. borealis. As shown in Fig. 10, the results of this study strongly indicate only one annual spawning period.

Oogenesis occurred earliest (January) in shrimp exposed to 6°C. A delay of five weeks to mid-February was recorded at 3°C. A further delay of ten weeks to mid-March was noted for shrimp in a high temperature regime of 9°C.

Ovarian maturation took from early March to mid-August at 6°C (5.5 months). In March 15% of the shrimp population were in the recovery phase, 53% were intermediate or early active, and 32% were ripening. Ripening continued throughout the spring and into the summer (Fig. 10; Appendix I, Tables 22 and 23). Except for the precocious release of eggs by two females in June, spawning pattern was similar in both years (Fig. 11; Appendix I, Table 24). Spawning began in late August, but major spawning occurred within a three-week period in September. The highest weekly incidence of synchronous spawning involved as much as 32% of the population. Minor spawning continued until early October. A total of 97% of the population spawned successfully. All specimens extruded their eggs within a 12-hour period on the day of spawning. A tendency was noted among multiparous females (22 and 23 mm CL) to spawn earlier than small primiparous (18 and

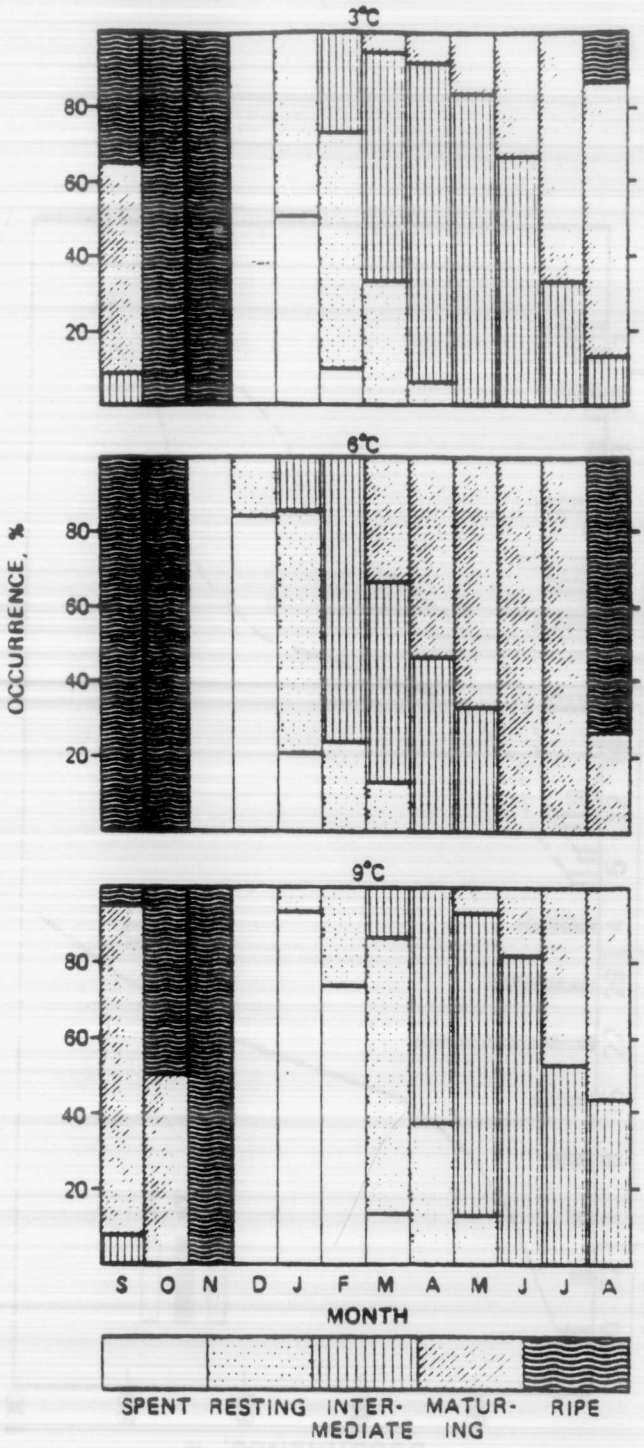


Figure 10. Reproductive cycle of Pandalus borealis in relation to temperature.

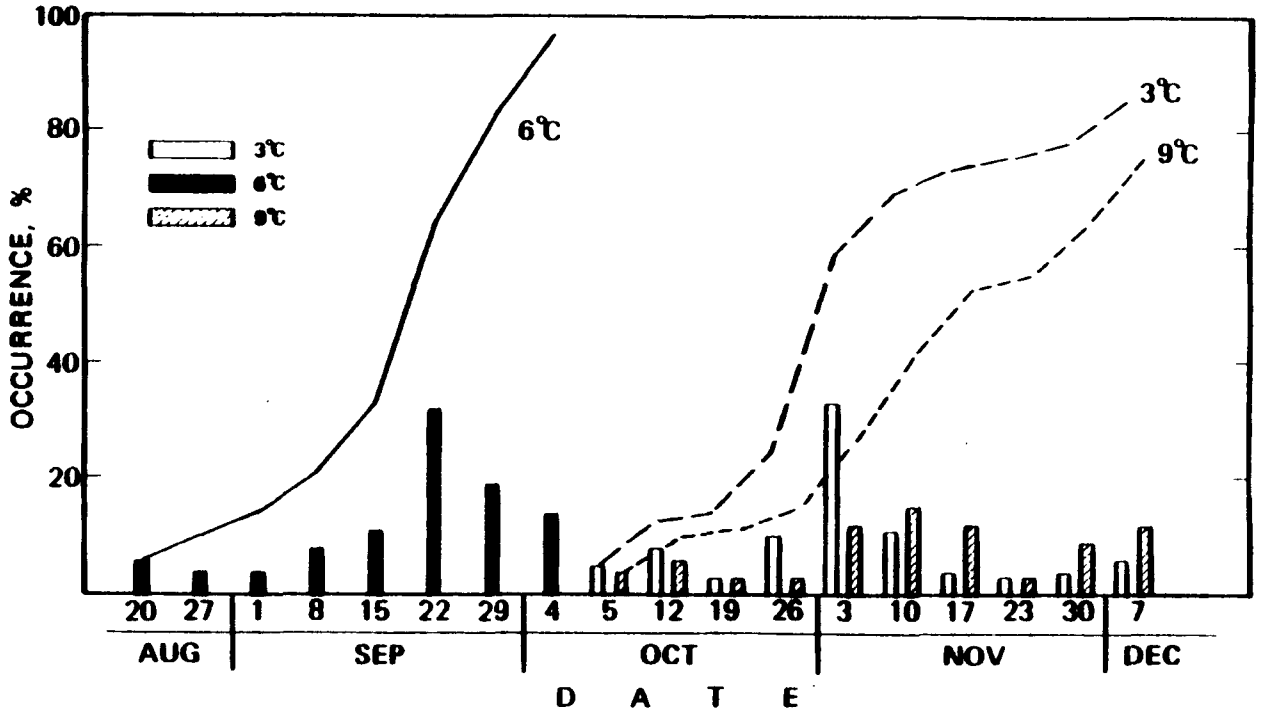


Figure 11. Time of spawning by Pandalus borealis in relation to temperature.

19 mm CL) and larger multiparous females (24 and 25 mm CL) (Fig. 12; Appendix I, Table 25).

Ovarian maturation occurred over a 6.5 month period among shrimp at 3°C, a month longer than at 6°C. In late March 35% of the shrimp population was recovering from the previous spawning season, 60% were intermediate or early active, and 5% were ripening. Spawning began in early October and continued until early December with major spawning occurring over a six-week period from late October through November. As was observed at 6°C, the highest incidence of synchronous spawning involved 32% of the population. Thus, spawning at 3°C began 4-5 weeks later and lasted two weeks longer than at 6°C. A total of 85% of the population spawned successfully (12% lower than that at 6°C). There was no precocious release of eggs. As at 6°C, egg extrusion did not take more than 12 hours and primiparous females (18 and 19 mm CL) tended to extrude their eggs later than multiparous females (20-25 mm CL).

Ovarian maturation at 9°C took place over a 5-month period from May through September. Major spawning occurred over a 6-week period from early November through early December, being two weeks later than at 3°C and six weeks later than at 6°C. In contrast to 3 and 6°C, two episodes of major spawning occurred. However, fewer than 15% of the population spawned during each outbrust. A total of only 75% of the population spawned successfully. There was no precocious release of eggs at 9°C.

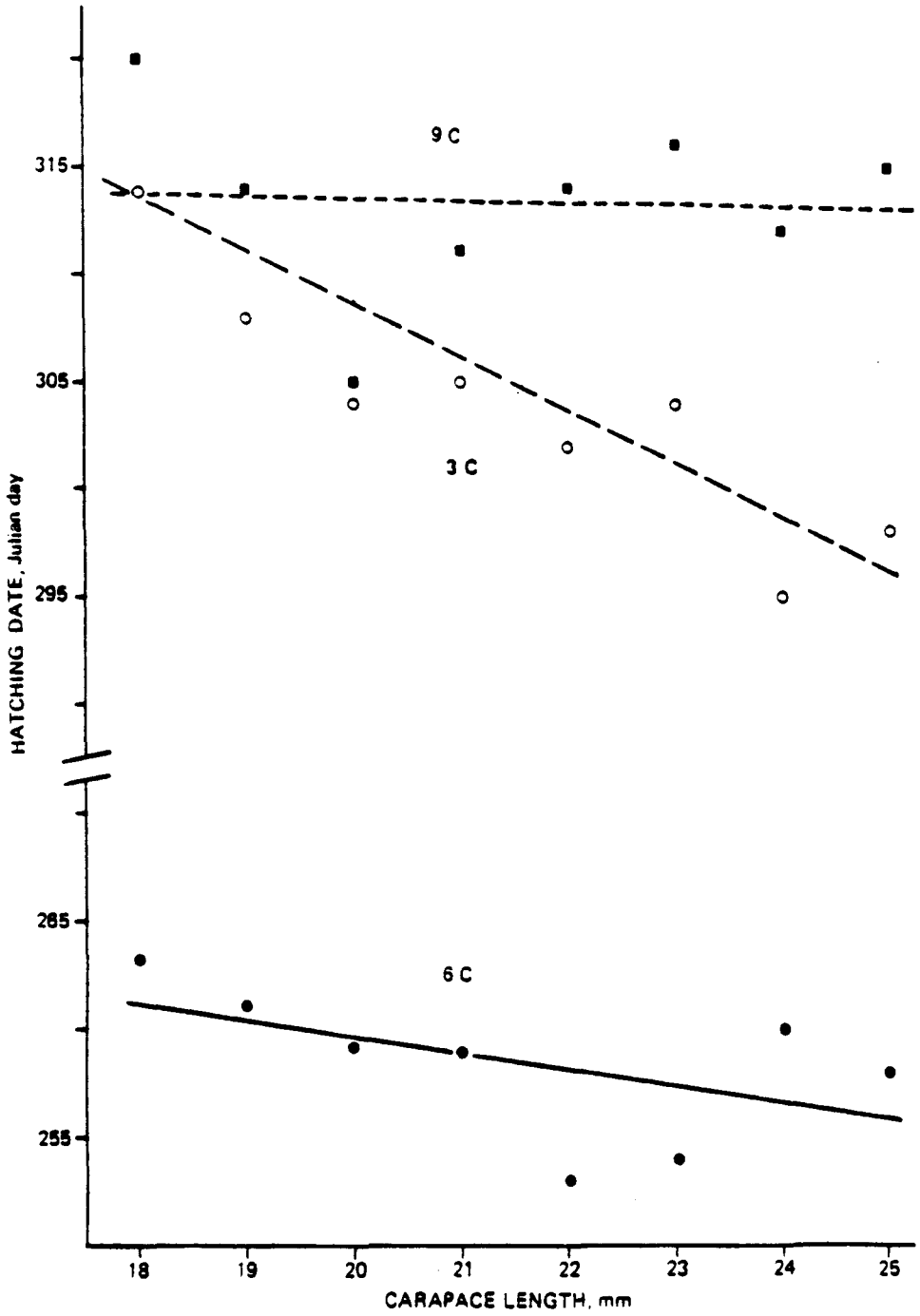


Figure 12. Spawning times of different size classes of Pandalus borealis at different temperatures.

As was observed at 3 and 6°C, egg release was confined to a 12-hour period. In contrast to 3 and 6°C, spawning time was not related to female size.

Mean time to spawning (± SD) over all the size classes was 258 ± 3 days at 6°C, 304 ± 6 days at 3°C and 313 ± 4 days at 9°C. Spawning at 6°C commenced significantly earlier than at 3 or 9°C ($F=449.4$, $P<0.0005$), but no significant differences were indicated between 3 and 9°C.

Spawning lasted 58-64 days ($\bar{X}=60.5$) at 3°C, 45-50 days ($\bar{X}=47.1$) at 6°C and 58-68 days ($\bar{X}=62.1$) at 9°C. Mean spawning duration was closely related to temperature ($F=65.1$, $P<0.0005$), but not female size ($F=0.7$, $P>0.25$). The shortest spawning duration at 6°C is statistically different from the longer duration at 3 and 9°C, but no significant difference exists between low and high temperatures ($P=0.05$).

In summary, the present results suggest that in a cold year, spawning will be delayed by up to a month and result in a 10% reduction in the number of spawning females. Similarly in a warm year, spawning will also be postponed by 4-6 weeks and breeding females reduced by as much as 20% (Table 2).

A comparison of oocyte types clearly demonstrated seasonal changes at the three temperatures. Oogonia and immature oocytes increase within a month following spawning at all three temperatures (Fig. 13), and are identical with those oocytes that would form the stock of immature ova by the following summer.

Table 2. Summary of spawning activity for Pandalus borealis held in the laboratory under different thermal regimes.

Spawning Activity	Temperature (°C)		
	3	6	9
Duration of ovarian development (days)	195	165	150
Time of first ovigerous female	Oct. 5	Aug. 14	Oct. 4
Proportion of ovigerous females on first ovigerous day (%)	3.8	1.3	2.5
Duration of spawning period (days)	61	47	62
Maximum proportion of ovigerous females (%)	85	97	75

Table 3. Occurrence of yolkless and atretic oocytes in Pandalus borealis during the 1980 and 1981 spawning seasons. Each value represents the mean of 80 observations

Temperature (°C)	Dates	Occurrence	
		Yolkless Oocytes (%)	Atretic Oocytes (%)
3	November 1980	13	2
	November 1981	9	2
6	September 1980	1	1
	September 1981	4	1
9	November 1980	24	1
	November 1981	24	1

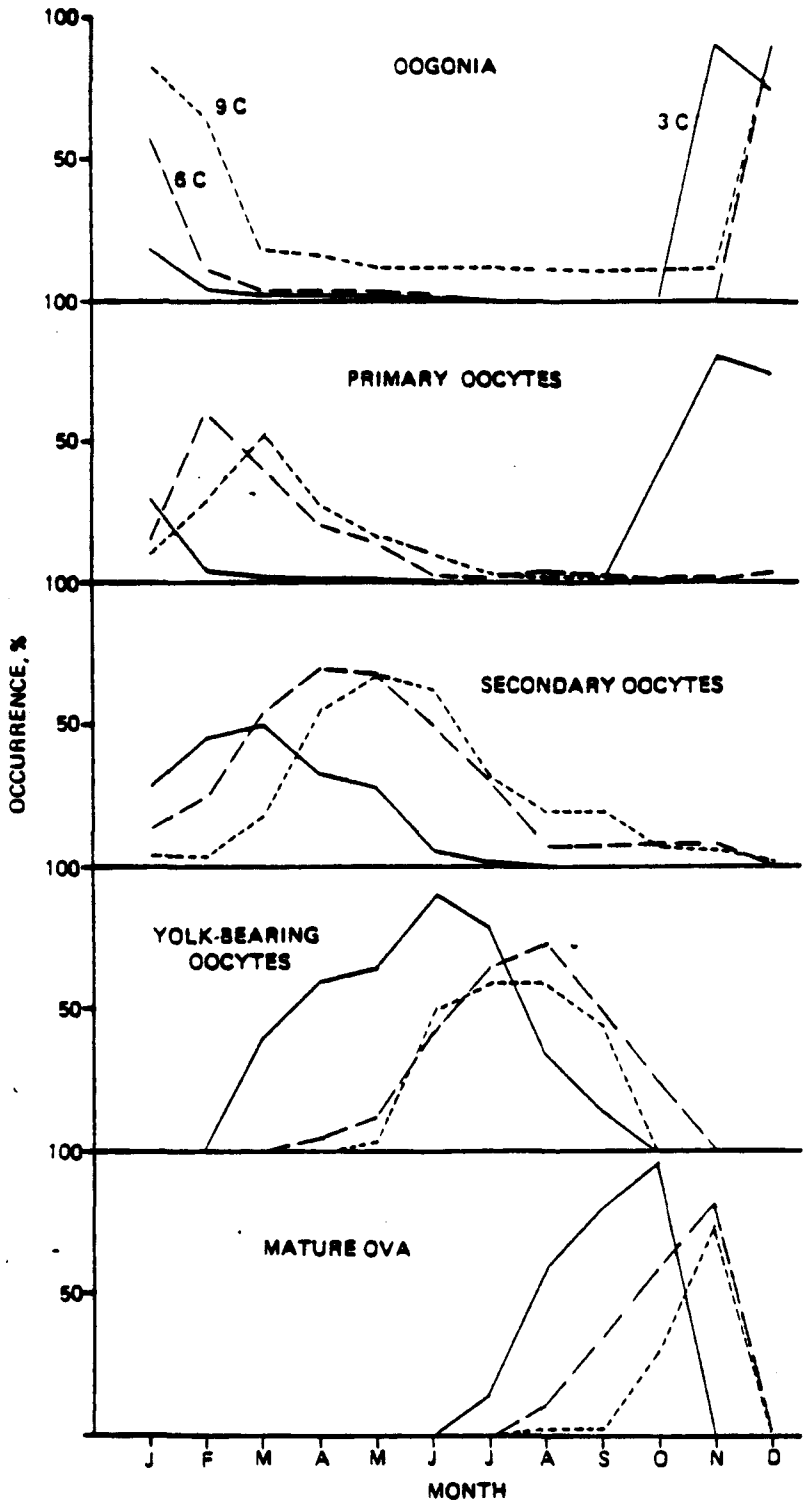


Figure 13. The change in developing ovaries of Pandalus borealis with time and temperature.

These data suggest a one year oocyte maturation period in P. borealis that is temperature-dependent.

A difference in oocyte size during the recovery phase of development was found. Oocyte sizes increased by 0.16 mm at 3°C, 0.14 mm at 6°C, and 0.12 mm at 9°C, showing a tendency toward larger sizes at low temperatures. The increase in oocyte size began earlier at 6°C (November-December) and a month later at 3 and 9°C (Fig. 14; Appendix I, Table 26). Rapid development of oocytes occurred at 3 and 6°C during a 3-month period from January to March. This is demonstrated by the increase in average oocyte size from 0.25 to 0.52 mm at 3°C and from 0.37 to 0.62 mm at 6°C. A comparable rate of oocyte development did not begin at 9°C until March. The proportion of ovaries that ultimately developed yolk was highest at 6°C (95-97%), intermediate at 3°C (83-85%), and lowest at 9°C (75%) (Fig. 13; Table 2; Appendix I, Tables 22 and 23). Thus, an increase in water temperature delays the initial phase of gametogenesis, but does not inhibit oocyte growth in later stages.

Fully developed ovaries (Table 1, Stage 4) were less common at both lower and higher temperatures. The percent occurrence of non-developing ovaries was 15% at 3°C and 25% at 9°C, compared with only 5% at 6°C.

Egg Production - Egg production increased with female size at all temperatures (Table 4). Mean egg number ranged between 1,018-2,495 at 3°C, 940-2,362 at 6°C, and 605-2,006 at 9°C.

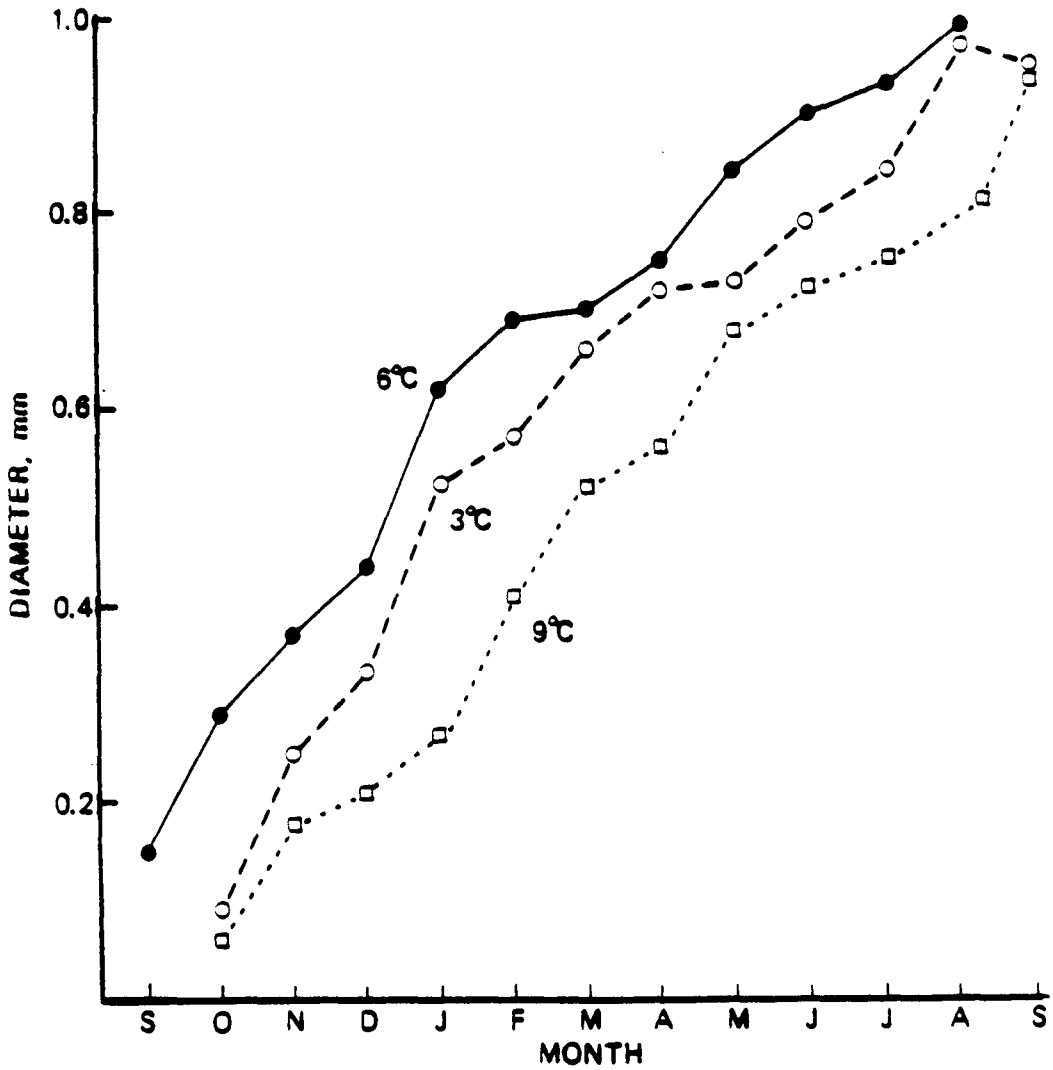


Figure 14. The change in oocyte diamters during ovarian maturation in Pandalus borealis at different temperatures.

Table 4. Relation between female size and clutch size in Pandalus borealis in relation to temperature. Each value represents the mean of a minimum of 20 observations. RB=Resurrection Bay.

Temperature (°C)	Female Size (CL mm)	Clutch Size X ± 75	Range	CV
3	18	1018 ± 75	764-1372	7.4
	19	1238 ± 89	995-1581	7.2
	20	1431 ± 110	1220-1741	7.7
	21	1645 ± 95	1398-1992	5.8
	22	1831 ± 106	1553-2009	5.8
	23	1941 ± 86	1655-2127	4.4
	24	2257 ± 115	1967-2447	5.1
	25	2495 ± 107	2288-2702	4.3
6	18	940 ± 92	751-1129	9.8
	19	1162 ± 106	1006-1318	9.1
	20	1343 ± 139	1160-1522	10.4
	21	1586 ± 125	1331-1811	7.9
	22	1728 ± 140	1453-1903	8.1
	23	1862 ± 102	1640-2087	5.5
	24	2128 ± 143	1885-2392	6.7
	25	2362 ± 131	2201-2640	5.0
9	18	605 ± 102	433- 777	16.9
	19	836 ± 129	647-1025	15.4
	20	1011 ± 119	842-1180	11.8
	21	1247 ± 141	1066-1428	11.3
	22	1402 ± 154	1148-1586	11.0
	23	1588 ± 131	1355-1741	8.3
	24	1830 ± 125	1585-2050	6.8
	25	2006 ± 127	1945-2267	6.3
RB	18	872 ± 138	630-1091	1.58
	19	1168 ± 175	812-1403	1.50
	20	1242 ± 172	1051-1514	1.39
	21	1465 ± 190	1163-1767	1.30
	22	1611 ± 180	1331-1894	1.12
	23	1802 ± 191	1512-2090	1.06
	24	2118 ± 206	1826-2382	9.73
	25	2314 ± 151	2104-2514	6.53

Considerable variability in clutch sizes between individuals of the same size occurred among shrimp at all temperatures. The coefficients of variance indicate that fecundity tends to fluctuate more widely in smaller than in larger females. This tendency toward greater variability in egg production among smaller shrimp is enhanced with increased temperature. Egg production was least variable at 3°C and greatest at 9°C, especially among the smaller shrimp. Egg production at 6°C was similar to that for P. borealis in Resurrection Bay (3.3-10.5°C; $\bar{X}$=6.3°C). The difference in the number of eggs was highly significant among the temperatures ($F=204.5$, $P<0.01$) and among the size classes ($F=817.9$, $P<0.01$). Only 22 and 23 mm shrimp showed no significant differences in egg numbers.

Figure 15 depicts a strong linear relationship between female size and mean number of eggs. While the slopes were almost identical among the three temperatures, the intercepts at 3 and 6°C were significantly different from that at 9°C at the 5% confidence level. The slopes indicate an increase in egg number at a rate of approximately 200 per 1 mm increase in carapace length, irrespective of temperature.

Embryonic Development - The mean time required by embryos of P. borealis to attain each of the five designated stages is shown in Figure 16. Mean time to hatching was 183 days at 3°C, 115 days at 6°C, and 105 days at 9°C. The relationship between temperature and developmental rate of shrimp eggs was best

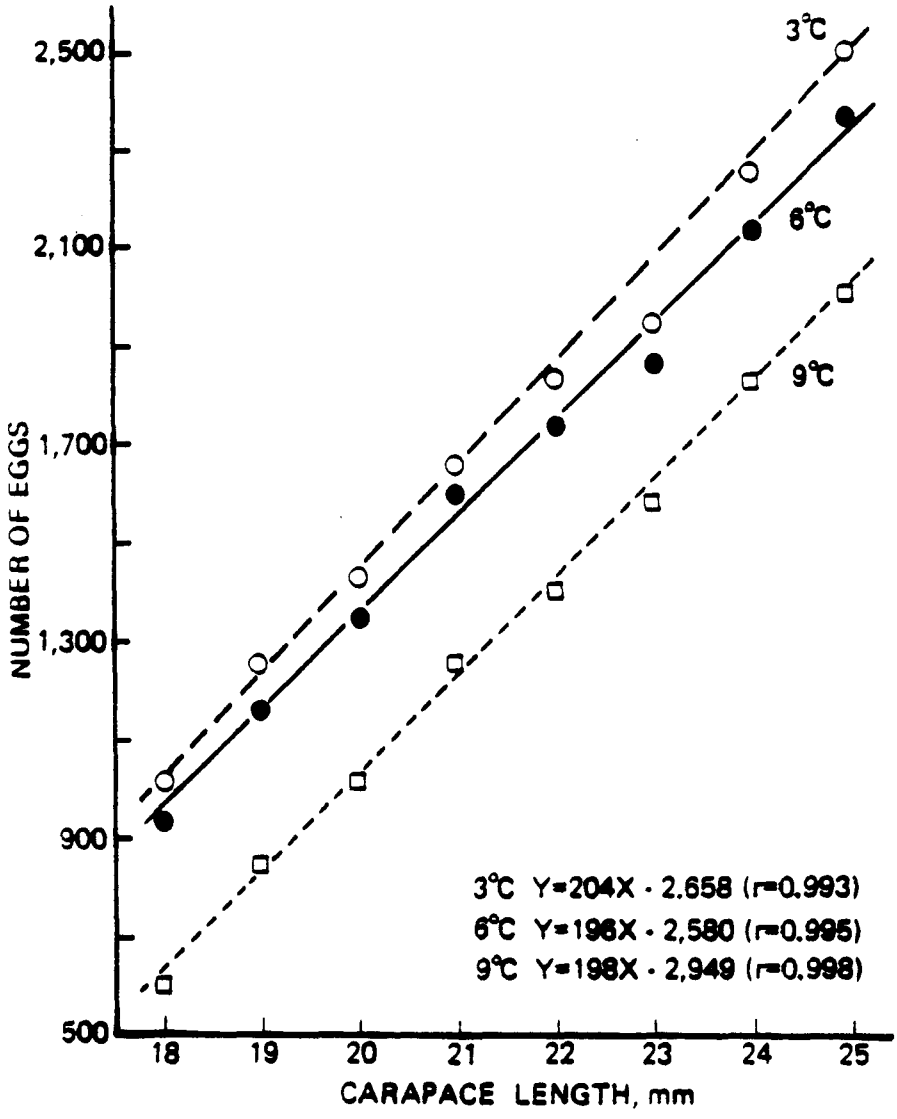


Figure 15. Relation of egg production to temperature and size in Pandalus borealis.

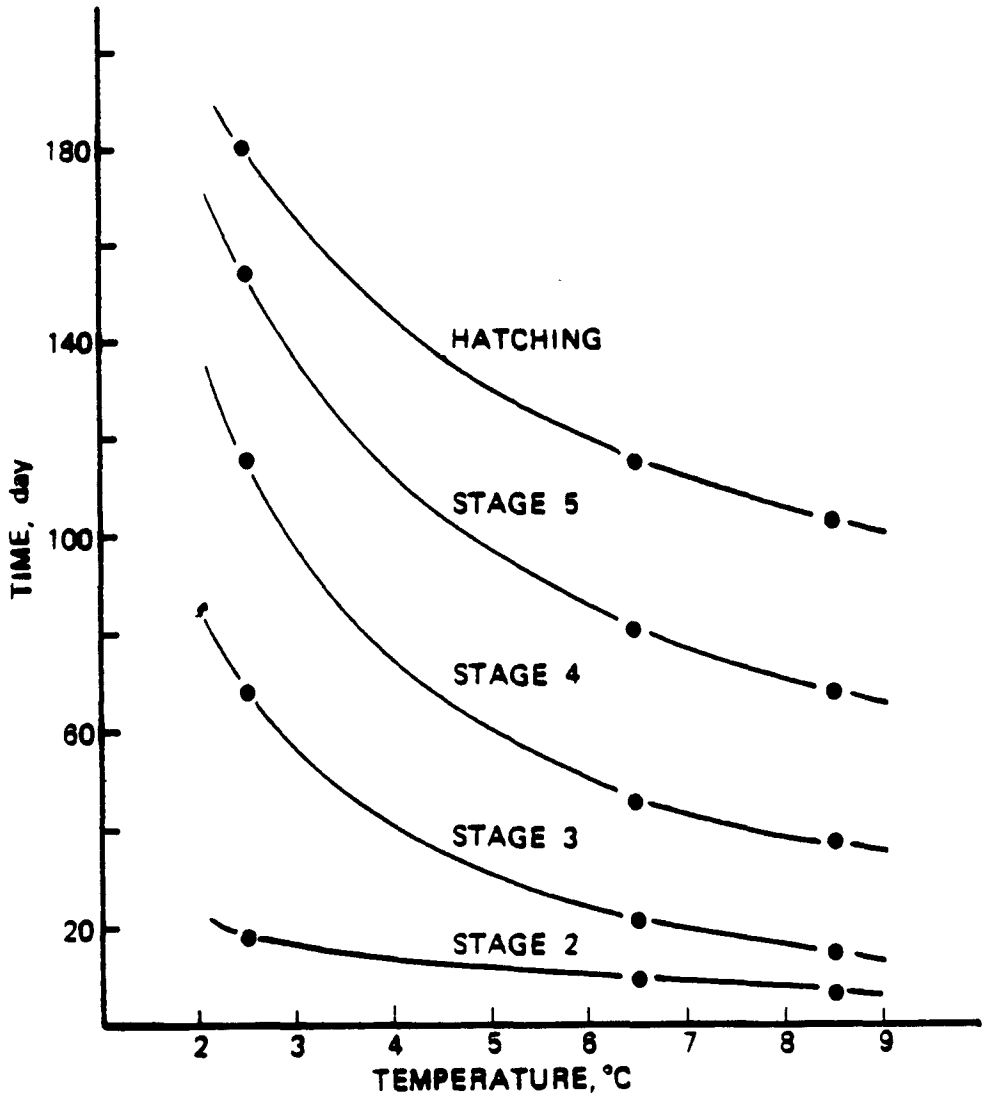


Figure 16. Effect of temperature on the time required to reach successive embryonic stages and on the time of larval hatching in Pandalus borealis.

described by the power function $D=aT^b$, where D is development time in days (from extrusion to 50% hatch), T=incubation temperature, a and b are constants. The difference in incubation time among the temperatures was statistically significant ($F=52.5$, $P<0.01$), and there was no correlation between female size and rate of egg development (Fig. 17).

Growth Rates of Developing Embryos - Table 5 shows the dimensions of newly fertilized eggs at spawning from shrimp exposed to different temperatures. Shrimp eggs ranged between 1.10 and 1.20 mm in length and between 0.78 and 0.90 mm in width.

Mean egg length at spawning for the range of size classes examined was 1.11 ± 0.02 mm at 3°C, 1.13 ± 0.01 mm at 6°C, and 1.18 ± 0.02 mm at 9°C. While mean egg lengths were not significantly different between 3 and 6°C, mean egg length at 9°C was significantly larger ($F=52.5$; $P=0.01$). However, there was no correlation between female size and mean egg length at spawning ($F=1.8$, $P<0.25$).

Mean egg width at spawning was 0.84 mm at 3°C , 0.85 mm at 6°C, and 0.86 mm at 9°C, indicating an increasing trend with increasing temperature as was observed in mean egg length. The difference among the means was significant ($F=14.8$, $P<0.01$). However, mean egg width at spawning was not correlated with female size ($F=1.5$, $P<0.25$).

Egg volume ranged from 0.397 to 0.478 mm^3. Mean egg volume was 0.41 mm^3 ± at 3°C, 0.42 mm^3 ± at 6°C, and 0.46 mm^3 ± at 9°C

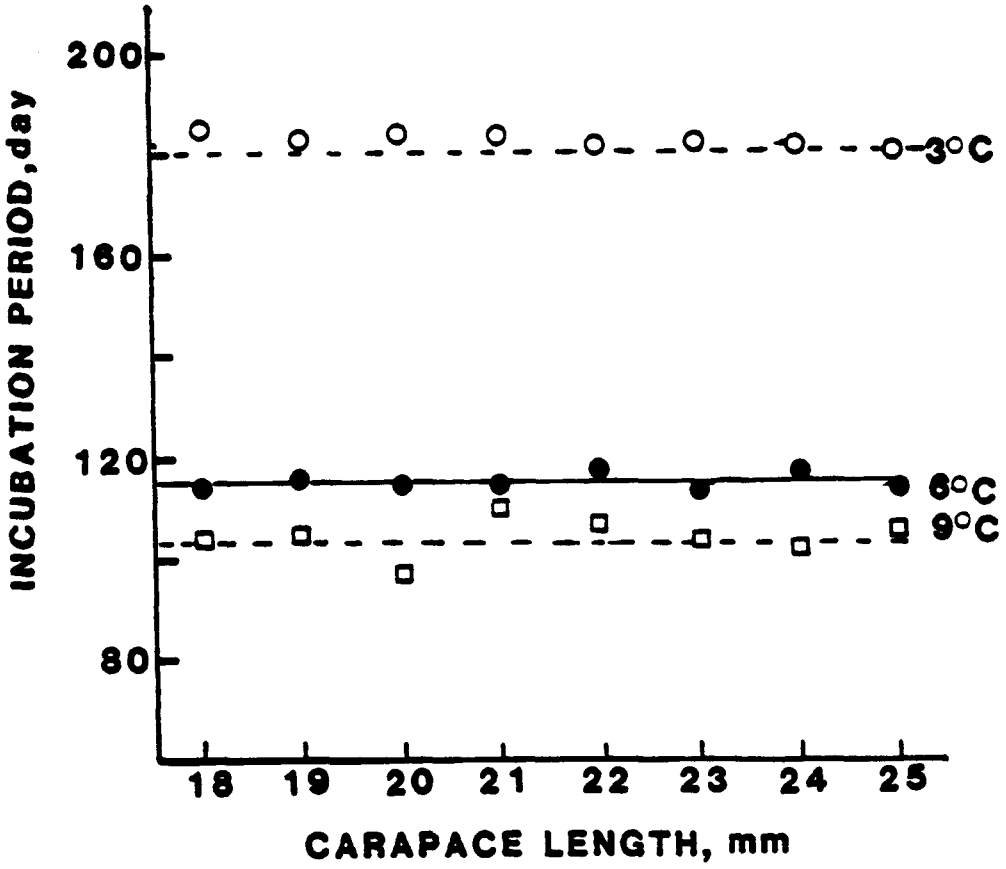


Figure 17. Mean larval hatching time by different size classes of Pandalus borealis at different temperatures.

Table 5. Relation of Pandalus borealis egg size (mm) at spawning to water temperature and adult size. Each value represents the mean of 500 egg measurements from ten shrimp from 1979-82. L=Length; W=Width; RB=Resurrection Bay

T°C		Carapace Length (mm)							
		18	19	20	21	22	23	24	25
3	L	1.12±0.02	1.10±0.02	1.11±0.02	1.12±0.04	1.11±0.05	1.11±0.04	1.10±0.03	1.10±0.01
	W	0.84±0.02	0.85±0.03	0.83±0.03	0.84±0.02	0.85±0.04	0.83±0.03	0.83±0.02	0.83±0.01
6	L	1.14±0.01	1.14±0.04	1.13±0.04	1.12±0.04	1.12±0.05	1.11±0.05	1.12±0.03	1.14±0.01
	W	0.85±0.02	0.84±0.02	0.85±0.01	0.84±0.03	0.86±0.03	0.84±0.02	0.86±0.02	0.84±0.03
9	L	1.17±0.02	1.20±0.02	1.18±0.04	1.19±0.04	1.18±0.03	1.17±0.04	1.16±0.05	1.15±0.04
	W	0.86±0.03	0.85±0.02	0.88±0.05	0.87±0.03	0.88±0.02	0.87±0.03	0.85±0.04	0.85±0.02
RB	L	1.14±0.02	1.12±0.04	1.12±0.01	1.13±0.05	1.11±0.04	1.12±0.03	1.10±0.05	1.13±0.02
(3-10)	W	0.86±0.02	0.87±0.03	0.84±0.01	0.83±0.02	0.85±0.03	0.82±0.03	0.85±0.02	0.83±0.03

(Fig. 18). Mean egg volume for shrimp from Resurrection Bay collected in September was 0.42 mm^3, intermediate between that obtained at 3 and 6°C. There was no relationship between female size and egg volume at the same temperature. The same was true for shrimp from Resurrection Bay. However, a significant difference was found between temperatures ($F=40.9$, $P<0.01$) with egg volume at 9°C significantly larger than at 3 and 6°C.

The influence of incubation temperature on size (length and width) of developing shrimp embryos is given in Table 6. The lower temperatures had a greater effect on the growth of developing embryos, and this effect was accentuated in the later stages, especially when the embryonic heartbeat was first observed (Stage 5). At 3°C, mean egg length increased markedly from 1.10 mm at spawning to 1.13 mm shortly before hatching. Similarly at 6°C, mean egg length increased from 1.12 to 1.28 mm, while mean egg width increased from 0.84 to 0.90 mm. At 9°C, mean egg length from spawning to hatching increased by only 0.04 mm. Decreased growth with a simultaneous increase in mean of days to reach the later embryonic stages occurred at 9°C (Table 7).

Figure 19 shows the change in egg volume with development. At 3°C, egg volume increased from 0.414 mm^3 at spawning to 0.568 mm^3 at hatching for a 37% increase in volume. Egg volumes increased by 30% at 6°C from 0.414 mm^3 at spawning to 0.543 mm^3 at hatching. In contrast to the lower temperature, egg volume at

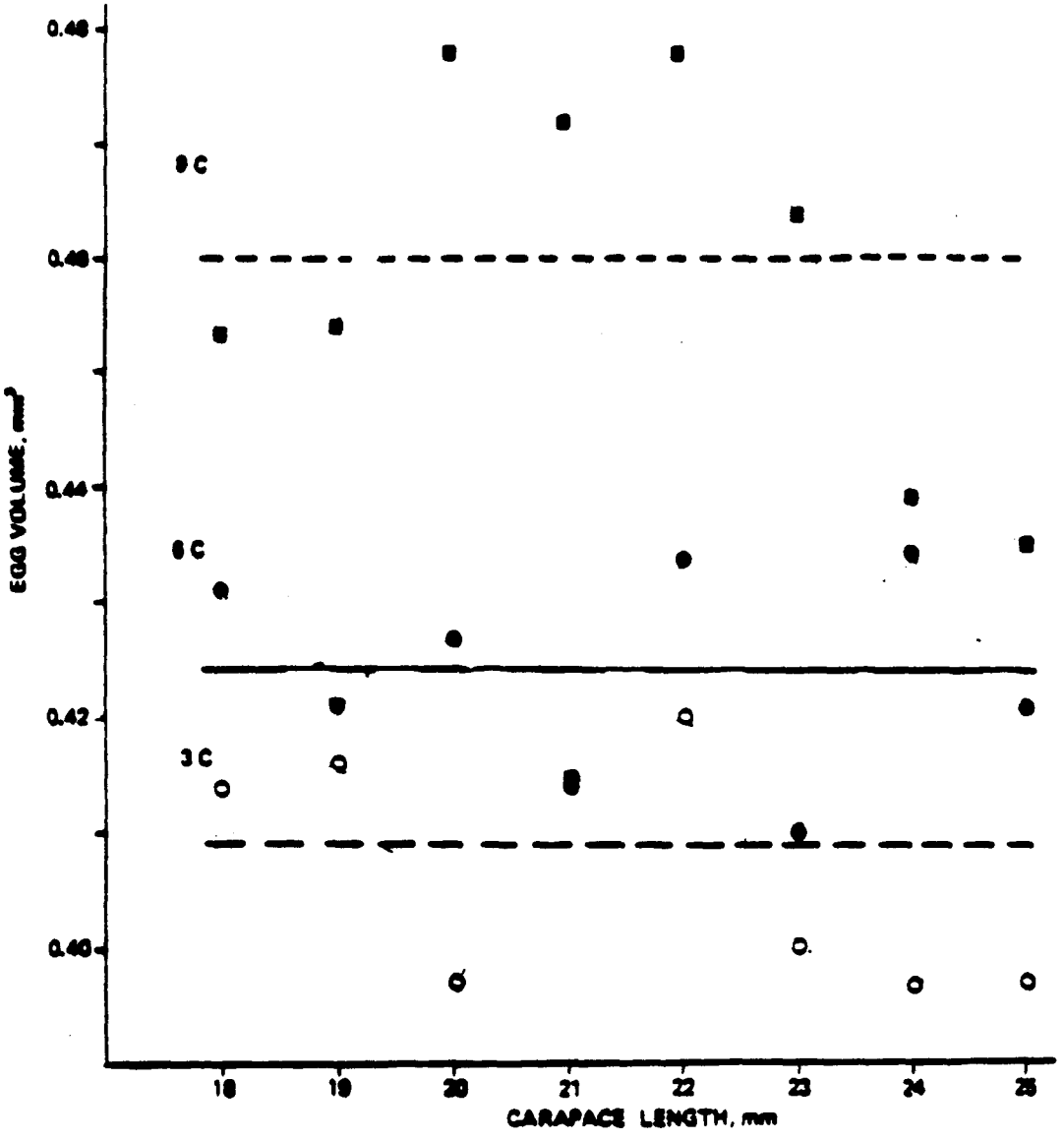


Figure 18. Relation of Pandalus borealis egg volume at spawning to temperature and female size.

Table 6. Influence of incubation temperature on size (mm) of developing eggs of Pandalus borealis from 1979-82. Each value represents the mean of 300 eggs. L=Length; R=Range; W=Width; RB=Resurrection Bay.

T°C		Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Hatching
3	L	1.10±0.01	1.12±0.02	1.15±0.03	1.20±0.07	1.26±0.09	1.31±0.10
	R	1.10-1.12	1.10-1.15	1.12-1.17	1.15-1.22	1.25-1.30	1.27-1.33
	W	0.83±0.02	0.83±0.01	0.84±0.03	0.86±0.02	0.88±0.02	0.91±0.04
	R	0.80-0.85	0.80-0.85	0.80-0.87	0.84-0.87	0.85-0.90	0.89-0.93
6	L	1.12±0.01	1.13±0.02	1.17±0.03	1.20±0.05	1.25±0.04	1.28±0.05
	R	1.10-1.14	1.11-1.20	1.12-1.23	1.17-1.22	1.18-1.27	1.20-1.31
	W	0.84±0.04	0.84±0.02	0.87±0.02	0.88±0.02	0.89±0.04	0.90±0.05
	R	0.78-0.87	0.80-0.89	0.83-0.90	0.83-0.90	0.85-0.90	0.85-0.92
9	L	1.18±0.03	1.19±0.03	1.20±0.03	1.20±0.06	1.21±0.08	1.22±0.07
	R	1.15-1.20	1.17-1.20	1.17-1.20	1.18-1.21	1.18-1.22	1.20-1.23
	W	0.86±0.04	0.86±0.03	0.86±0.03	0.86±0.05	0.87±0.05	0.88±0.08
	R	0.80-0.90	0.83-0.90	0.84-0.90	0.85-0.90	0.85-0.91	0.85-0.92
RB	L	1.12±0.03	1.14±0.02	1.18±0.04	1.21±0.08	1.25±0.08	1.28±0.10
	R	1.10-1.16	1.14-1.22	1.10-1.20	1.15-1.23	1.18-1.28	1.20-1.30
	W	0.83±0.04	0.83±0.03	0.86±0.03	0.88±0.04	0.89±0.03	0.89±0.06
	R	0.75-0.85	0.79-0.85	0.81-0.87	0.82-0.90	0.84-0.90	0.85-0.91

Table 7. Developmental and growth rates of Pandalus borealis eggs in relation to incubation temperature.

Incubation Temperature (°C)		Developmental Stages					
		1	2	3	4	5	Hatching
3	No. of Days Between Stages	18	50	47	39	29	
	% Increase in Egg Length	1.8	2.7	4.4	5.0	4.0	
	% Increase in Egg Volume	1.76	5.20	9.41	9.89	11.15	
6	No. of Days Between Stages	9	12	25	32	36	
	% Increase in Egg Length	0.9	3.5	2.3	4.2	2.4	
	% Increase in Egg Volume	0.72	11.27	4.96	6.37	4.83	
9	No. of Days Between Stages	6	9	23	31	35	
	% Increase in Egg Length	0.9	0.9	0	0.8	0.8	
	% Increase in Egg Volume	0.88	0.87	0	3.23	3.13	

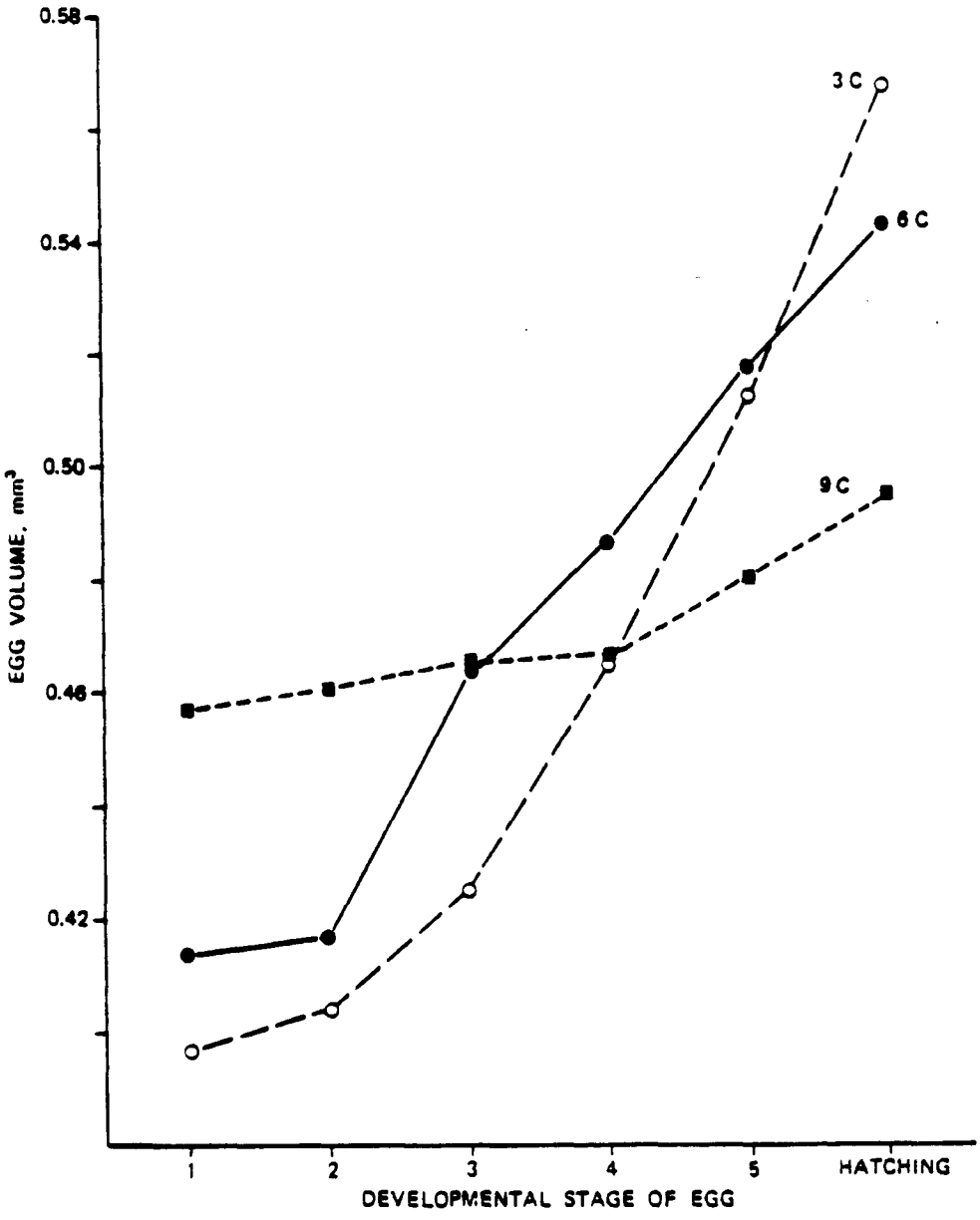


Figure 19. Influence of incubation temperature on size of developing eggs of Pandalus borealis.

9°C increased by only 8% from spawning (0.457 mm^3) to hatching (0.495 mm^3). The difference in final egg volume between temperatures was significant ($F=7.2$, $P<0.01$). Thus, egg volume at 9°C was largest at spawning and smallest at hatching. The reverse was seen at 3°C.

Table 7 shows the changes in length and volume of eggs during development. At 3°C, the increase in length was greatest from Stage 3 to Stage 4, while the greatest change in volume occurred during Stage 4 to Stage 5, with a tendency for greater increases to occur at the later stages. In contrast, the largest increase in length at 6°C occurred between Stage 4 and 5, and the largest volume increase occurred earlier between Stage 2 and Stage 3. Unlike the lower temperatures, little change in egg size occurred at 9°C until Stage 4.

Mean daily growth rate of developing shrimp embryos is given in Table 8. The changes in volume were highest at 3°C. In contrast, changes in growth rate in length were largest at 6°C. At 9°C, increases in both length and volume were lowest overall. Thus, changes in daily growth rates with temperature were related to differences in egg size at spawning and the length of the incubation period.

Egg Loss - Estimated egg losses incurred by different sizes of shrimp at three temperatures are presented in Table 9. Egg loss was highly variable, ranging between 0.5 and 23%. While an exceptionally high egg loss rate occurred among 22 and 23 mm

Table 8. Daily growth increments of length and volume of *Pandalus borealis* eggs during the period from spawning to hatching at different temperatures.

Growth Rate	Temperature, C		
	3	6	9
Duration, day	180	115	103
Length increment, % day	0.117	0.139	0.039
Volume increment, % day	0.997	0.314	0.037

Table 9. Relation between female size and egg loss (%) in Pandalus borealis at different temperatures and incubation times. Each value represents the mean of a minimum of 20 observations. RB=Resurrection Bay.

Temp (°C)	Carapace Length	Incubation Period		Cumulative
		Post-Spawning	Pre-Hatching	
3	18	8.8	3.8	12.6
	19	9.5	3.2	12.7
	20	9.0	4.7	13.7
	21	12.1	2.0	14.1
	22	16.9	6.1	23.0
	23	19.9	3.0	22.9
	24	9.6	3.4	13.0
	25	9.7	2.7	12.4
		$\bar{X}$ 11.9	$\bar{X}$ 3.5	$\bar{X}$ 15.5
6	18	1.0	0.5	1.5
	19	2.2	0.2	2.4
	20	5.3	0.4	5.7
	21	3.4	0.3	3.7
	22	5.9	0.1	6.0
	23	6.1	0.1	6.2
	24	1.5	0.5	2.0
	25	4.4	0.3	4.7
		$\bar{X}$ 3.3	$\bar{X}$ 0.3	$\bar{X}$ 4.0
9	18	0.3	0.2	0.5
	19	0.2	0.3	0.5
	20	6.1	0.2	6.3
	21	4.3	0.1	4.4
	22	5.5	0.1	5.6
	23	3.2	0.2	3.4
	24	2.4	0.1	2.5
	25	3.9	0.1	4.0
		$\bar{X}$ 3.2	$\bar{X}$ 0.2	$\bar{X}$ 3.4
RB	18		25	
	19		27	
	20		35	
	21		38	
	22		40	
	23		42	
	24		39	
	25		44	
			$\bar{X}$ 36.3	

females at 3°C, there was no overall relation between egg loss and female size ($F=0.9$, $P<0.25$). Egg loss averaged 15.6% at 3°C over a 180-day period, 4.0% at 6°C over 115 days and 3.4% at 9°C over 103 days. The differences in mean egg loss among the three temperatures were highly significant ($F=53.9$, $P<0.01$), with egg loss 4-5 times greater at 3°C than at 6 or 9°C. Daily egg loss rate is estimated to be 0.087% at 3°C, 0.035% at 6°C and 0.033% at 9°C. This is approximately equivalent to a 1.5 egg loss per day at 3°C and one egg loss per two days at 6 and 9°C for an average sized female.

Larval Hatching Success - Hatching rates varied between 30 and 79% among the different sizes of shrimp at different temperatures. Mean total hatching rates were generally consistent at 60-62% at the three temperatures for all size classes (Table 10). There were no significant differences in the total hatching rate among the three temperatures ($F=0.4$, $P<0.25$) and female size ($F=0.1$, $P<0.25$). An unusually low hatching rate was noted among 21 mm females at 3°C. Mean viable hatching rate ranged between 49 and 55% with no significant differences among temperatures ($F=0.8$, $P<0.25$) and size classes ($F=0.6$, $P<0.25$). Thus, hatching rates do not differ greatly in relation to incubation temperature and female size.

Larval loss averaged 7% at 3°C, 12% at 6°C, and 9% at 9°C. There were no significant differences in adult size and larval loss at the temperatures examined ($F=0.9$; $P=0.01$). At 6 and 9°C,

Table 10. Relation to larval hatching success in Pandalus borealis to temperature and adult size. Each value represents the mean of a minimum of 40 observations made from 1979-1982.

Carapace	3°C			6°C			9°C		
length mm	Hatching (%) total	viable	loss	Hatching (%) total	viable	loss	Hatching (%) total	viable	loss
18	63.4	52.2	11.2	44.3	37.4	6.9	62.7	53.3	9.4
19	60.6	54.4	6.2	56.4	45.2	11.2	33.1	30.1	3.0
20	51.2	45.3	5.9	74.3	59.6	14.7	54.4	48.1	6.3
21	32.3	29.5	2.8	78.8	51.2	27.6	72.6	55.6	17.0
22	68.4	64.6	3.8	72.0	58.9	13.1	65.2	54.3	10.9
23	76.6	68.7	7.9	48.1	36.2	11.9	72.7	60.9	11.8
24	65.2	57.3	7.9	68.5	58.7	9.8	55.6	48.4	7.2
25	78.8	69.8	9.0	51.4	47.4	4.0	60.4	51.2	9.2
$\bar{X}$	62.1	55.2	6.8	61.9	49.3	12.4	59.6	50.2	9.4
SD	± 14.9	± 13.4	± 2.8	± 13.3	± 9.4	± 7.0	± 12.7	± 9.1	± 4.2

larval loss was high among medium sized females (20-23 mm). In contrast, a low incidence of larval loss occurred among medium sized females at 3°C, especially among 21 mm shrimp. This is in contrast to the exceptionally high values among 21 mm shrimp at 6 and 9°C. Excluding these unusual values, mean larval loss is recalculated to be 7.4% at 3°C, 10.2% at 6°C, and 8.3% at 9°C. Therefore, the rate of larval loss at hatching falls in nearly the same range (7-10%) regardless of female size or temperature.

As larval hatching periods were identical in both years at all three temperatures, the data was pooled from the two years of observation. Larval sizes varied between 0.92 and 1.6 mm (Fig. 20). Mean larval size at hatching was 1.49 mm at 3°C, 1.41 mm at 6°C and 1.09 mm at 9°C. The differences in larval size among the three temperatures were found to be significant ($F=122.7$, $P<0.01$), with a 50% difference in size between 3 and 9°C. No relation was found between larval size and female size within the same temperature ($F=1.6$; $P<0.25$).

A summary of the effects of water temperature on the reproductive processes of Pandalus borealis is given in Table 11.

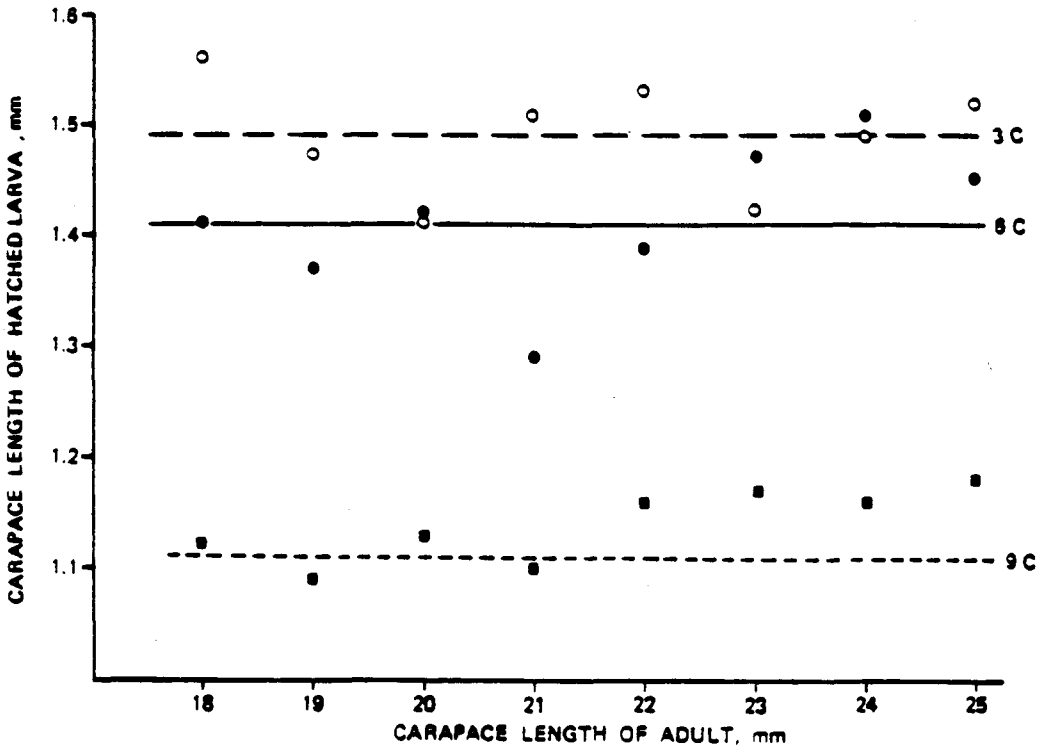


Figure 20. Mean size of newly hatched Pandalus borealis larvae as a function of incubation temperature and adult size.

Table 11. Temperature effects on the reproductive processes of Pandalus borealis.

Reproductive Processes	Temperature °C		
	3	6	9
Maximum number of ovigerous females	Medium	High	Low
Egg production	High	High	Low
Embryonic development	Long	Medium	Short
Egg loss	High	Low	Low
Size of larvae	Large	Large	Small
Larval hatching success	Same	Same	Same
Larval viability	High	Medium	Low

DISCUSSION

In assessing the effects of environmental factors on mussels, Bayne (1976) stated that the measurable biological responses should show a quantitative relationship with altering environmental stimuli. This study demonstrated that effects of temperature on oogenesis were reflected in spawning activity. The early, short spawning at 6°C contrasted sharply with the delayed and prolonged spawning at 3 and 9°C. It is known that in colder waters, P. borealis spawn earlier and the ovigerous period lasts longer (Rasmussen 1954; Horsted and Smidt 1956; Allen 1959; Butler 1964; Haynes and Wigley 1969; Ivanov 1969; Ito 1976). If an inverse relationship between temperature and spawning time is the general trend, spawning at 3°C would be expected to begin earlier than at 6 or 9°C. Contrary to expectations, earliest spawning occurred at 6°C. The similarities in spawning time and duration between 3 and 9°C were confirmed in two spawning cycles. There are few reports of a similarity in spawning pattern between high and low temperatures. Stickney and Perkins (1977) reported that ovaries of captive P. borealis mature faster at 6°C than at colder (4°C) or warmer (8°C) temperatures. Although the low and high temperatures employed by these authors were not the same as in this study, the present results appear to confirm their observations. From the marked variations in spawning with small changes in temperature observed in this study, it appears that P. borealis reproduction is affected by narrow thermal tolerances.

Prevailing temperatures of P. borealis areas in Ishikari Bay off Hokkaido are reportedly 0.4-0.5°C (Kojima et. al. 1969), 0.1-2.1°C off the west coast of Kamchatka (Kitano and Yorita 1978), and 0.4-0.8°C in the Sea of Japan (Ito 1976). Berenboim (1982) demonstrated that P. borealis in the Barents Sea cannot reproduce at temperatures below -1.0°C, the apparent boundary of the "sterile zone". Thus, temperatures in the Sea of Japan and off the west coast of the Kamchatka peninsula are close to the lower limit of thermal tolerance for reproduction. Although spawning below 3°C was not examined here, it is likely that spawning in colder waters will be delayed and prolonged more than those at 3°C. Spawning is indicated to occur from February to May in these regions, and the year-round occurrence of ovigerous shrimp have been reported (Abe 1977).

Spawning has not been reported to occur at an ambient temperature of 9°C. However, it is likely that P. borealis encounter temperatures close to 9°C in the southern limit of their geographical distribution. They are known to occur off British Columbia where bottom temperatures range between 7.4 and 11.1°C (Bulter 1964). Whether high temperatures in the natural habitat result in delayed spawning as suggested by this study awaits confirmation.

Low and high temperatures caused a high incidence of sterile females in contrast to almost full fertility at intermediate temperatures. The variation in sterility with temperature is

likely to be an important factor in determining the reproductive potential of the natural population. The high sterility rate at 9°C may be related to the upper limiting temperature of this species of 8-11°C (Rasmussen 1953; Allen 1959; Butler 1964). The delay and prolongation of spawning at low and high temperatures suggest that the difference in fertility is due to an inhibitory effect on the process of egg formation. The existence of an inhibitory effect on egg formation by temperature has not been previously demonstrated. The high occurrence of undeveloping ovaries at low and high temperatures may be ascribed to (1) reduced numbers of maturing oocytes per ovary, or (2) to a reduction in egg size, or (3) to a combination of these factors. A reduction in the number of maturing oocytes may result from either (1) a reduction in the number of yolkless oocytes entering vitellogenesis or (2) an increase in resorption of yolk-bearing oocytes (atretic). To examine the first possibility, the relation of yolk-bearing, yolkless as well as atretic oocytes to temperature was analyzed. A marked decrease in yolk-bearing oocytes was found at 3 and 9°C. In contrast, the proportion of yolkless oocytes which did not progress to vitellogenesis increased at 3 and 9°C (Table 5). However, no relationship was found between the number of atretic oocytes and temperature. Therefore, reduced ovarian development at 3 and 9°C was due to a reduction in the number of oocytes which accumulated yolk. Therefore, the high incidence of sterility at 3 and 9°C is

derived from a reduction in the number of oocytes that undergo the vitellogenic phase of yolk development. Thus, these observations appear to support a suppressive role for low and high temperatures on egg formation.

It is generally recognized that fecundity is regulated by the interrelated effects of body length, metabolism, level of food supply, and temperature (Prosser and Brown 1961). The positive linear relationship between body length and clutch size observed in this study confirms that the number of eggs in a brood depends on the size of the female as has been reported for amphipods, euphausiids, mysids, and other decapods (Balasundaram and Pandian 1981). The variation in egg number with size has been well documented for P. borealis from various areas (Rasmussen 1953; Allen 1959; Apollonio and Dunton 1969; Haynes and Wigley 1969; McBride 1979; Stickney 1980; Ito 1976), but the reported egg numbers and fecundity-size relationships vary. Egg counts varied from 500 to 3000 (Kurata 1957), 1700 to 2600 (Sakurai et. al. 1958), 1000 to 7000 (Yamada and Naiki 1976), and from 579 to 4904 for 23-33 mm (Ito 1976) in the Sea of Japan. McBride (1979) obtained egg counts of 68 to 2054 for pink shrimp in Kachemak Bay, Alaska. P. borealis in southern Norway were reported by Rasmussen (1953) to carry from 460 to 3400 eggs. Allen (1959), in the North Sea off the coast of Northumberland, obtained egg counts from 300 to 1500 eggs. In the Gulf of Maine, Haynes and Wigley (1969) reported egg counts of 800 to 3400 eggs

for 22.2 to 31.0 mm shrimp. When compared with these values, the range of clutch sizes in the present study for P. borealis in Resurrection Bay is similar to those reported from Kachemak Bay and Northumberland, but fewer than that in the Japan Sea, southern Norway and the Gulf of Maine. The size ranges and the average number of eggs per individual of P. borealis in Resurrection Bay were greater than those reported from the North Sea (Allen 1959) and Norwegian waters (Rasmussen 1953) but less than those for the Gulf of Maine (Haynes and Wigley 1969).

Previous authors refer to the observed number of eggs in the natural habitat, without reference to developmental stage and prevailing water temperatures, as fecundity. It seems desirable to distinguish the observed number of eggs immediately after spawning as apparent fecundity from that determined shortly before hatching as potential fecundity. It is clear that the difference between apparent fecundity and potential fecundity depends largely upon temperature, female size and duration of the ovigerous period. Further, it is apparent that the number of eggs at spawning is predetermined by the temperature during oogenesis. Therefore, it is important that prevailing water temperatures are known when determining the fecundity of P. borealis.

Apollonio and Dunton (1969) found fecundity to vary significantly in regions of the Gulf of Maine that differed in temperature. They concluded that the variation in egg production

was directly related to the degree of thermal stratification in different areas of the Gulf. The results of this study support Apollonio and Dunton's conclusion, and demonstrate that total population fecundity may vary with temperature by as much as 20-40%. Moreover, the greatest variability in egg production occurs among smaller sized shrimp, especially at higher temperatures. The Gulf of Alaska experienced a cold spell in the early 1970s, reaching a low of a little over 2°C below normal in 1975. The cold spell of four years was followed by four years of temperatures 2 to 3°C above normal (Niebauer 1978). It has been reported that during this period the mean size of shrimp in the Kodiak fishery declined to the 22-23 mm size class (Jackson 1968, 1979, 1980). Thus, it is inferred that the contribution of larger shrimp to stabilizing the population may have been lost. Consequently, the burden of rebuilding stocks is increasingly placed on the reproductive potential of the less fecund, smaller shrimp whose fecundity varies the greatest with temperature.

There are few reports on the developmental rates of pink shrimp eggs at different temperatures. Stickney and Perkins (1977) estimated incubation time for P. borealis eggs to be 167 days at 3°C, 120 days at 6°C and 93 days at 9°C. These values are similar to the present results of 180 days at 3°C, 115 days at 6°C, and 103 days at 9°C. The ovigerous period of P. borealis in the Japan Sea and off the west coast of Kamchatka reportedly lasts 8-12 months (Kojima et. al. 1969; Ito 1976; Kitano and

Yorita 1978). If, as reported, the representative temperatures of these regions are 0.5-1°C throughout the year, and applying the empirical equation given here, the time required to hatch at 0.5 and 1°C is estimated to be 12.5 months and 9 months, respectively. Ivanov (1969) showed that the ovigerous period is 6.5 months at 4°C in the Gulf of Alaska and 7.5-8 months at 1.5°C in the Bering Sea. The estimated ovigerous period from the present equation is 4.8 months for the Gulf of Alaska and 7.6 months for the Bering Sea. Except for the Gulf of Alaska, these values coincide closely with the reported ones.

P. borealis in captivity were observed to have lost their developing eggs. The rate of egg loss varied in relation to temperature and duration of incubation. Ito (1976) showed a decrease in mean egg number with increasing development in the Japan Sea. He estimated egg loss to be 500 eggs during the six-month period. This is equivalent to a 2.8 egg loss per day at 0.4-0.8°C which is nearly twice as great as the 1.5 egg loss per day at 3°C in this study. Although it is known that a high mortality of P. borealis eggs in the laboratory is caused by infection due to parasites (Apollonio and Dunton 1969; Stickney and Perkins 1977, 1979; Stickney 1978), no such infection was observed in this study. Balasundaram and Pandian (1982) ascribed the loss of crustacean eggs during incubation to mechanical severance, erosion, abrasion and volumetric expansion from water uptake. Severance and abrasion coupled with increased rearing

density can be discounted as the main reason for egg loss in this study as the shrimp were all kept at the same density. Neither does swimming activity of captive P. borealis appear to cause egg loss, since the shrimp were mostly immobile at the lowest temperature. Although the present study did not show a relation between the rate of egg loss and egg volume, it is likely that the increase in egg volume causes a greater egg loss at 3°C since the largest increases in egg volume and growth rate occurred at the lowest temperature.

An unusually high occurrence of egg loss was seen among 22 and 23 mm females at 3°C. While the reason for these anomalous values is not known, they may be attributed to a difference in swimming behavior. Medium sized shrimp were more active in swimming than were small and large sized shrimp. Thus, the occurrence of size-specific egg loss may be explained by a prolonged incubation period coupled with size-specific behavior differences.

Higher than normal egg loss was reported for P. borealis in Pavlof Bay and the shrimping areas off the Shumagin Islands during the cool year of 1971 (Alaska Department of Fish and Game 1972). It was determined that as many as 84% of the females had lost all of their eggs prior to hatching and 25% of the females still carrying eggs had only partial clutches. Horsted and Smidt (1956) estimated egg loss of 95% among ovigerous P. borealis in West Greenland fjords during the cold year of 1953-54. The

occurrence of major egg loss at 3°C in this study suggests that the occurrence of temperatures below 3°C in Alaskan waters during the egg-carrying period could have substantial effects on the dynamics of shrimp populations. Spawning areas with water temperatures of less than 3°C would be expected to experience fluctuations in larval production as a result of minor annual differences in temperatures. Therefore, the availability of temperatures of less than 3°C to 6°C during the ovigerous period may, to a major extent, determine the northern limits of distribution and abundance of P. borealis in Alaskan waters.

Optimum temperatures for the reproductive processes examined here were consistently within a narrow range of 3-6°C. The maximum percentage of females reproducing successfully occurred among shrimp at 6°C. Highest egg production and survival were seen among shrimp at 6°C. Shrimp at 3°C had the highest larval hatching rates and produced the largest larvae. Larvae hatched from eggs incubated at 3°C were more viable than those from eggs incubated at higher temperatures. Spawning shrimp apparently avoid temperatures below 3°C (Ivanov 1969). The largest concentrations of pink shrimp in the Gulf of Alaska during the egg-carrying period were found at the 3.4 to 5.5°C range. The bathymetric distribution of P. borealis during the ovigerous period thus is associated with an avoidance of supra- and infra-optimal incubation temperatures.

The results obtained in this study can be applied to the culture of P. borealis. In artificial propagation, the acquisition of healthy seed at a maximal level is of prime importance. Eggs or larvae must be produced at the desired time. The results of this study provide information on the timing of occurrence of eggs and larvae from maturing P. borealis at a given temperature range. Empirical equations established here allow the prediction of incubation period, egg and larval size, and the number of eggs and larvae for a given female size. The holding of females around 6°C is most appropriate as the duration of spawning can be minimized and the number of fertile females and large eggs maximized at this temperature. In addition, egg loss can be reduced. In comparison, 9°C appears to be advantageous only when accelerated egg development is desirable. Although larvae were successfully reared at 12°C (Omi and Yamashita 1976; Wienberg 1982), a high temperature is not recommended due to its retarding effect on spawning. Moreover, fewer and smaller sized larvae can be expected at 9°C. In contrast, both the number and size of newly hatched larvae can be maximized by decreasing temperatures. However, this has to be balanced against incurring greater egg loss at temperatures below 6°C. While the survival and growth rates of larger sized larvae were not compared with those of small size larvae, low incubation temperatures were found to increase larval survival and growth

rates, irrespective of rearing temperatures and feeding levels (see Chapter 3).

CHAPTER 3

LARVAL STUDIES

Combined Effects of Temperature and Food Availability on Larval Survival, Growth and Development

It has been argued that year class strength is determined during the early stages of larval life rather than by the total number of eggs produced by the spawning stock, or by mortality during the more advanced stages of the pre-recruitment phase (Hjort 1926; Beverton 1962; Nikolsky 1962; Hempel 1963). Correlations have been found between year class strength and environmental conditions such as temperature and food availability in a number of fisheries (for review see Gulland 1965). Such correlations may have only limited value however, since they shed little light on the direct effects of environmental factors on the larvae.

Previous work on decapod crustacean larvae was directed at deriving culture techniques and establishing optimum levels of environmental factors such as temperature and salinity (Templeman 1936; Bookhout 1964; Knowlton 1965; Costlow 1971; Sanifer 1973; Rothlisberg 1979; Johns 1981a; Wienberg 1982). Few studies examined the influence of food availability on larval survival (Brick 1974; Bigford 1978). In the oceanic environment, the amount, size and temporal occurrence of suitable planktonic food organisms influence the size of year classes in decapod and fish

crustacean populations (Nakazawa 1912; Ishimaru 1936; Lasker 1975, 1981; Hunter 1976).

In nature many environmental factors act simultaneously. To test the hypothesis that food availability is a determinant of larval survival, the relationship of larval survival and food availability was examined within the range of temperatures encountered by larvae at sea. Specifically, this study sought to determine rates of survival that might be expected under suboptimal conditions of food availability, and the extent that temperatures influence larval survival under suboptimal food conditions.

Adequacy of Plantonic Foods

The availability of food of the proper quality and quantity is important to the development of planktonic larvae. The feeding habits of Pandalus borealis larvae have been studied by Lebour (1922) and Stickney and Perkins (1981). The early zoeal stages of P. borealis feed predominantly on diatoms. In the Gulf of Alaska, larval hatching occurs from March to May when temperatures increase from 3 to 7°C, and microflagellates are replaced by diatoms and dinoflagellates as the dominant phytoplankton groups (Barr 1970; Niebauer 1980; Horner et. al. 1973). To insure initial survival of the larvae, food must be available at this time.

One objective of this part of the study is to evaluate the adequacy of naturally occurring phytoplankton as food for the

larvae of Pandalus borealis. However, the intent was not to define the precise food value of algal species or to determine quantitatively the amounts of algal food required for survival and normal growth, but to examine larval survival given various densities of phytoplankton.

Starvation Resistance

Successful feeding by planktotrophic larvae is essential for survival. Surprisingly, little is known about resistance to and adaptation of larvae to lack of suitable prey. The potential to resist starvation is considered to be dependent upon various physiological and physical factors, including temperature which is the most important factor controlling metabolism (for review see Anger and Dawirs 1981).

The questions I address in this section are: 1) How long can larvae P. borealis survive without feeding? 2) Is there any larval stage which can complete development under conditions of starvation? 3) How long must an early larva feed in order to molt successfully to the next stage? and 4) How does early starvation affect larval feeding?

MATERIALS AND METHODS

General Methods. All larvae used in this study were hatched in the laboratory from females exposed to different temperatures for over a year. The day free-swimming individuals hatched was called day 1, the day after as day 2, and so forth. Newly

hatched zoeae were transferred by wide-bore pipette to experimental containers within 12 hours of hatching.

Antibiotics were not used as they can accelerate or retard larval development (Brick 1974). Although no significant bacterial contamination was evident, there may have been some bacterial development adding a separate source of food for the larvae. The extent of bacterial contribution to the nutrtion of P. borealis larvae was not considered.

Seawater was passed through a 1 µm HA Millipore filter and stored at 3, 6 and 9°C for 12 hours prior to use as culture water. Thus there was no abrupt change in water temperature and salinity (33 ppt) imposed on the larvae during daily water change.

Larval cultures were maintained in controlled temperature rooms on a photoperiod approximating 14 hours light (20 lux) and 10 hours dark. Lights were timed to go on following sunrise so that diffuse light entering the windows increased gradually in intensity as the sun rose, and thereby avoiding the imposition of abrupt light or dark changes on the larvae.

In preliminary tests, larvae were cultured in a range of test vessels and stocking densities. Survival rates were highest among larvae reared in 600 ml polyethylene beakers. There were no significant differences in survival and growth between stocking densities of 1 zoea/100 ml and 1 zoea/20 ml of water. However, larval mortality rates increased markedly at densities of greater than 1 zoea/20 ml of water. This was due to

cannabalism during later stages. Thus, 600 ml polyethylene beakers were selected as the standard culture vessel with 1 zoea/20 ml of water was the standard rearing density.

All larval experiments were carried to the early post-larval or juvenile stages whenever possible. Water in the beakers was changed daily. The larvae were inspected at the same time of day when exuvia, mortalities, and uneaten food were removed and molts, deaths, and temperature were recorded. Criterion for death was the complete absence of a heartbeat. Only the presence of an exuvium was accepted as evidence of molting. Molting was considered to have occurred the day on which the cast-off exoskeleton was found. Survival and growth rates have a potential error of plus or minus 0.5 day as larvae also died and molted during the night.

Larval stages were classified into five zoeal stages as described by Haynes (1979). (See glossary under zoea for identifying features of the zoeal stages.) Carapace lengths of each larva was measured (±0.01 mm) with an occular micrometer after larvae were anaesthesized in 2% urethane (ethyl carbamate).

Food Levels. All the zoeae used in these experiments hatched from eggs incubated at 3, 6 or 9°C. Replicate cultures from each incubation temperature were then grown at 3, 6 or 9°C on different levels of feeding as follows:

a. Satiation diet: consisted of four algal species, namely, Tetraselmas, Phaeodactylum, Isochrysis and Skeletonema,

(density of 3 X 10^4 cells l^{-1}) and 500, 750, and 1000 Artemia salina nauplii at 3, 6, and 9°C, respectively. The San Francisco Bay strain of Artemia nauplii was used in this study as it has been shown to be the preferred strain of Artemia for decapod larval culture (Forster and Wickins 1967; Reeve 1969; Bookhout and Costlow 1970; Wickins 1972; Gallagher and Brown 1975; Rothlisberg 1979). These amounts represent four to five times the estimated minimum daily metabolic requirements of newly hatched larvae (see Paul and Nunes 1983 on respiratory metabolism of P. borealis larvae) and are an order of magnitude above the minimum prey densities required to insure successful prey capture (see section on predation rates). As the larvae grew, Artemia nauplii were grown to larger sizes on high concentrations of the four algae. Mixed sizes (1 to 3 days after hatching) of Artemia were then added in the amounts previously mentioned to all containers with surviving larvae.

b. Adequate diet: consisted of the same four algal species (density of 1.5 X 10^4 cells l^{-1}) as well as 150, 200, and 250 Artemia salina nauplii at 3, 6, and 9°C, respectively. Mixed sizes of larger-sized Artemia were fed to the later stages of those larvae still surviving as previously described. The number of Artemia added are slightly above the estimated minimum daily metabolic requirements of stage 1 zoeae and the required prey densities.

c. Marginal diet: consisted of 5 X 10^2 cells l^{-1} of the same four algal species plus 75, 100, and 125 Artemia nauplii at 3, 6, and 9°C, respectively. The same number of larger-sized Artemia were added to the diet of older larvae. These amounts represent approximately one-half the minimum metabolic requirements of newly hatched zoeae and are approximately 50% of the required prey densities.

Values obtained for each incubation temperature/rearing temperature/food level combination included:

1) survivorship of larvae on a daily and stage basis

2) rate of development expressed as the mean number of days to reach successive stages

3) growth for a particular zoeal stage

Estimation of Experimental Error. Larval Survival at each of 27 temperature/food level combination possesses three components of error: 1) sampling, 2) counting, and 3) response error due to inherent biological variability among individual larvae. To determine the significance of differences between individual combinations, the 95% confidence intervals for a single observation were estimated using a three-factor (temperature, food level, replicate cultures) analysis of variance. Twenty identical cultures of 10-day old survivors with a density of 1 zoea/20 ml were reared at 9°C and fed ad libitum. The 95% confidence intervals for a single observation was

estimated as ±11.8% by taking the square root of the mean standard error (MSE=36.2105) and multiplying by 1.96.

Adequacy of Planktonic Foods.

All the algal species employed in these experiments occur in Alaskan waters with the exception of the naked dinoflagellate, Tetraselmas (Horner et. al. 1973; K. Coyle, pers. comm.). Six single species and five mixed species comprised the diets supplied to the shrimp larvae:

Single-species Diets

1. Gonyaulax spp. (dinoflagellate) 35-45 µm (diameter)
2. Isochrysis galbana (diatom) 5 X 3 µm (diameter)
3. Phaeodactylum tricornutum (diatom) 7 X 21 µm (diameter)
4. Skeletonema costatum (diatom) 10 µm (diameter)
5. Tetraselmis spp. (dinoflagellate) 9 X 8 µm (diameter)
6. Thalassiosira spp. (diatom) 168 µm (diameter)

Mixed-species Diets	Ratios
1. Gonyaulax:Tetraselmis	1:1
2. Isochrysis:Phaeodactylum	1:1
3. Phaeodactylum:Tetraselmis	1:1
4. Isochrysis:Tetraselmis	1:1
5. Isochrysis:Phaeodactylum:Skeletonema	1:1:1

To minimize the variability inherent in these experiments, all the larvae used came from the same two females. Experiments were conducted at 3 and 6°C simultaneously. Algal food was supplied from stock cultures of the same age and growth medium.

Concentrations of algal food were 5 X 10^2 and 3 X 10^4 cells per liter. These concentrations are approximately equivalent to those encountered in Alaskan waters prior to and during a spring bloom, respectively (Horner et. al. 1973; Schandelmeier and Alexander 1981). Algal concentrations were determined using a photo-electronic counter or by counting an aliquot with a haemocytometer. Stock cultures were then diluted to give the desired experimental densities.

The larvae were reared in 600 ml polyethylene beakers at each of 22 temperature and diet combinations. They were reared at 3 and 6°C in temperature controlled rooms on a photoperiod of 14 hours light (300 lux) and 10 hours dark.

A second set of experiments compared the survival and growth of shrimp larvae at 6°C fed different algal and/or animal diets as follows:

a. plant diet: three algal species that occur in Alaskan waters, namely, Gonyaulax, Phaeodactylum and Skeletonema at concentrations of 3 X 10^4 cells per liter in a 1:1:1 ratio.

b. mixed plant and animal diet: the same three algal species as above at concentrations of 2 X 10^4 cells per liter plus Artemia salina nauplii at a density of 2000 per liter.

c. animal diet: Artemia salina nauplii at a density of 4000 per liter.

A third set of experiments determined how soon after hatching shrimp larvae require other sources of food in addition

to phytoplankton to reach metamorphosis. Shrimp zoeae were first fed Artemia nauplii at a density of 2000 per liter in addition to a plant diet of Gonyaulax, Phaeodactylum and Skeletonema at concentrations of 2×10^4 cells per liter at hatching, upon reaching ZII or ZIII.

A total of 50 shrimp zoeae were reared at each temperature and diet combination. The number of surviving larvae were counted, larval developmental stages identified, and carapace lengths measured every three to five days. Survival, growth and developmental rates were determined for each combination of temperature and diet.

Starvation Resistance.

All zoeae used in the experiments hatched at ambient temperature ($\bar{x}$ = 6°C) between 0100 and 0800 hours of the same day from two females. Twenty-five newly hatched zoeae were placed in polyethylene beakers (12.5 cm high, 90 mm diameter) containing 500 ml of 33% seawater passed through a 1 um HA Millipore filter. Larvae were kept in temperature controlled rooms on a photoperiod approximating 14 hours light (20 lux) and 10 hours dark. Water was changed daily. Experiments were terminated when all larvae had either died or reached the second juvenile stage.

Experiment 1. Early Starvation. Larvae were first fed following 4, 6, 8 or 10 days of starvation and reared at 3, 6, and 9°C. These periods of starvation were the equivalent of from 20 to 100% of the duration of the first zoeal stage at the

different temperatures. At the end of each starvation period, 2000 Artemia nauplii were added with each daily water change. Older larvae that had survived at the different temperature and starvation combinations were fed 500 larger sized Artemia. These Artemia nauplii had been growing for a week on a mixed diet of the diatoms Isochrysis galbana, Phaeodactylum, Skeletonema and Thalassiosira and the dinoflagellate Tetraselmis. Control groups of larvae were reared at the same temperatures and fed ad libitum from day 1. Two groups were reared at each of the temperature and starvation combinations. Survival data resulted from one group of larvae and growth data from the second group. Dead larvae were removed and recorded during daily water change. The carapace length of larvae from the second group was measured every two days to compare their growth with those from the control group.

Experiment 2. Prolonged Starvation. Newly hatched zoeae were placed in beakers containing 500 ml of 1 ξm filtered seawater without food at 3, 6, 9, and 12°C. Maximal survival time under starvation at the different temperatures was observed. Since larvae hatching late in the season encounter temperatures above 9°C, larval resistance to starvation at 12°C was also examined.

Experiment 3. Late Starvation. Newly hatched larvae were reared at 3, 6, and 9°C on a satiation diet of two-day old Artemia nauplii that had been previously feeding on a mixed diet

of algae. The zoeae were then starved upon attaining zoeal stages II, III, IV and V.

Experiment 4. Amount of Feeding Required for Early Survival. Stage 1 zoeae were fed the first 4, 6, 8 or 10 days after hatching. Two thousand Artemia nauplii were added during daily water change where appropriate. The actual number of Artemia nauplii ingested on a daily basis were not determined. Rather, amount of feeding was defined as the number of days at good feeding conditions.

Experiment 5. Early Starvation and Larval Feeding. Newly hatched zoeae were placed in 600 ml polyethelene beakers (12.5 cm high, 9 cm diameter) containing 500 ml of seawater passed through a 1 µm HA Millipore filter. Zoeae at each temperature of 3, 5.5 and 8°C were initially fed at 0, 2, 4 or 6 days following hatching. Prey consisted of live copepods and copepodids of the genera Acartia, Pseudocalanus, Metridia and Oithona. These zooplankters were taken from Resurrection Bay, retained on a 0.35 mm^2 screen, and picked out by a wide-bore pipette under a dissecting microscope.

Prey densities consisted of 20, 40, 60, 80 and 100 organisms per liter. In all experiments the prey items were counted individually by hand under a dissecting microscope. Mean length of prey items was 0.75 mm ± 0.2 mm. Similar concentrations of zooplankton occur to 200 mm in the Gulf of Alaska from March through July (T.R. Cooney, pers. comm.).

Predation rates were calculated as the difference between the number of copepods initially present and those remaining after a 24-hour period. Two control beakers containing copepods but no shrimp larvae were used to check the accuracy and reliability of the counting method. All copepods in the control beakers were accounted for during the recount. Analysis of variance was employed to examine the relationship of feeding success to temperature, starvation period and prey density.

RESULTS

Larval Survival. Deaths occurred mostly at the time of molting during the early zoeal stages with fewer deaths during the intermolt phase and after ZIV. Lowest mortality occurred among larvae reared at 9°C at all levels of feeding and all incubation temperatures. Of those larvae reared at 9°C, those that hatched from eggs incubated at 3°C showed the lowest mortality. An analysis of variance showed significant differences in survival between temperatures and between levels of feeding at 1% level. A Duncan Multiple Range test indicates that of the three parameters, rearing temperatures had the greatest effects on larval survival.

Effects on Larvae from Eggs Incubated at 3°C - Among larvae incubated at 3°C, mortalities decreased with increasing temperatures irrespective of feeding level (Fig. 21). Survival rate among larvae fed ad libitum was 92% at 3°C, 88% at 6°C, and 92% at 9°C. It was noted that no mortality occurred after ZII. Although mortality patterns were similar at all three temperatures, significant differences in survival rates were found among larvae reared on suboptimal levels of feeding. Mortality rates for larvae reared on an adequate level of feeding decreased steadily from 36% at 3°C, 32% at 6°C and 24% at 9°C. At 3°C the greatest mortalities occurred during ZII and ZIII. No mortalities occurred past ZIV. Similarly at 6°C, the greatest mortalities occurred at ZII and ZIII. Mortalities continued to

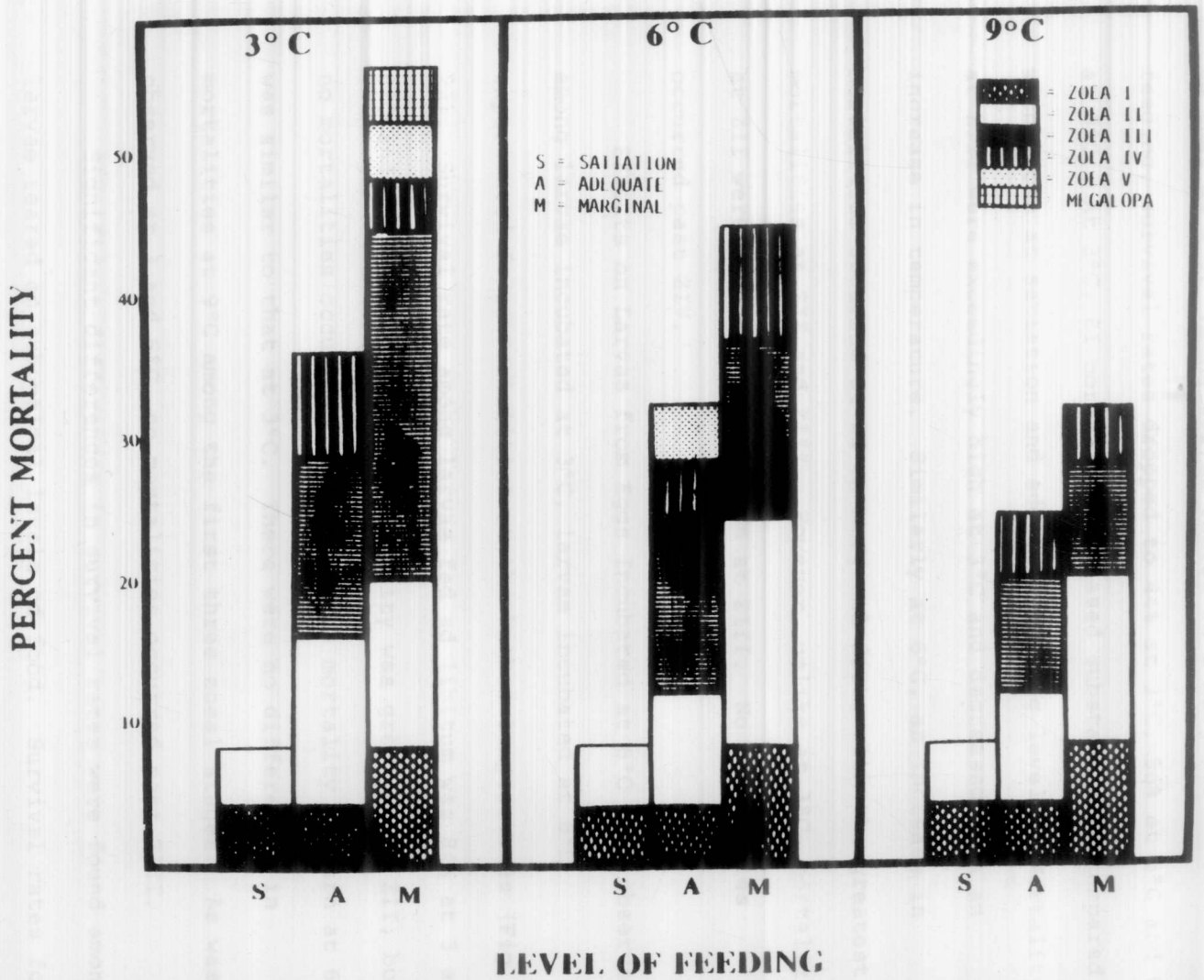


Figure 21. Mortality of Pandalus borealis larvae with an incubation temperature of 3°C and reared under different temperatures and food levels.

occur until ZV at 6°C. The mortality pattern at 9°C was similar to that at 3°C. Among larvae reared on a marginal level of feeding, survival rates dropped to 44% at 3°C, 56% at 6°C and 68% at 9°C. At 3°C, ZI mortality increased substantially compared with those at satiation and adequate feeding levels. Mortality at ZIII were exceedingly high at 3°C and decreased with an increase in temperature. Similarly at 6°C, an increase in mortalities occurred at ZI on marginal diets with the greatest mortalities at ZII and ZIII. However, unlike at 3°C, mortalities at ZII were slightly higher than at ZIII. No mortalities occurred past ZIV.

Effects on Larvae from Eggs Incubated at 6°C - As observed among larvae incubated at 3°C, larvae incubated at 6°C experienced fewer mortalities at the higher temperatures (Fig. 22). Survival rate among larvae fed ad libitum was 84% at 3 and 6°C and 88% at 9°C. At 3°C, mortality was greatest at ZII, but no mortalities occurred past ZIII. The mortality pattern at 6°C was similar to that at 3°C. There were no differences in mortalities at 9°C among the first three zoeal stages. As was observed at 3 and 6°C, no mortalities occurred past ZIII.

Significant differences in survival rates were found among larvae reared on suboptimal levels of food. Survival rates for larvae reared on an adequate level were 68% at 3°C, 64% at 6°C and 80% at 9°C. At 3°C mortalities at ZI and ZII doubled compared with those at satiation feeding levels, but no

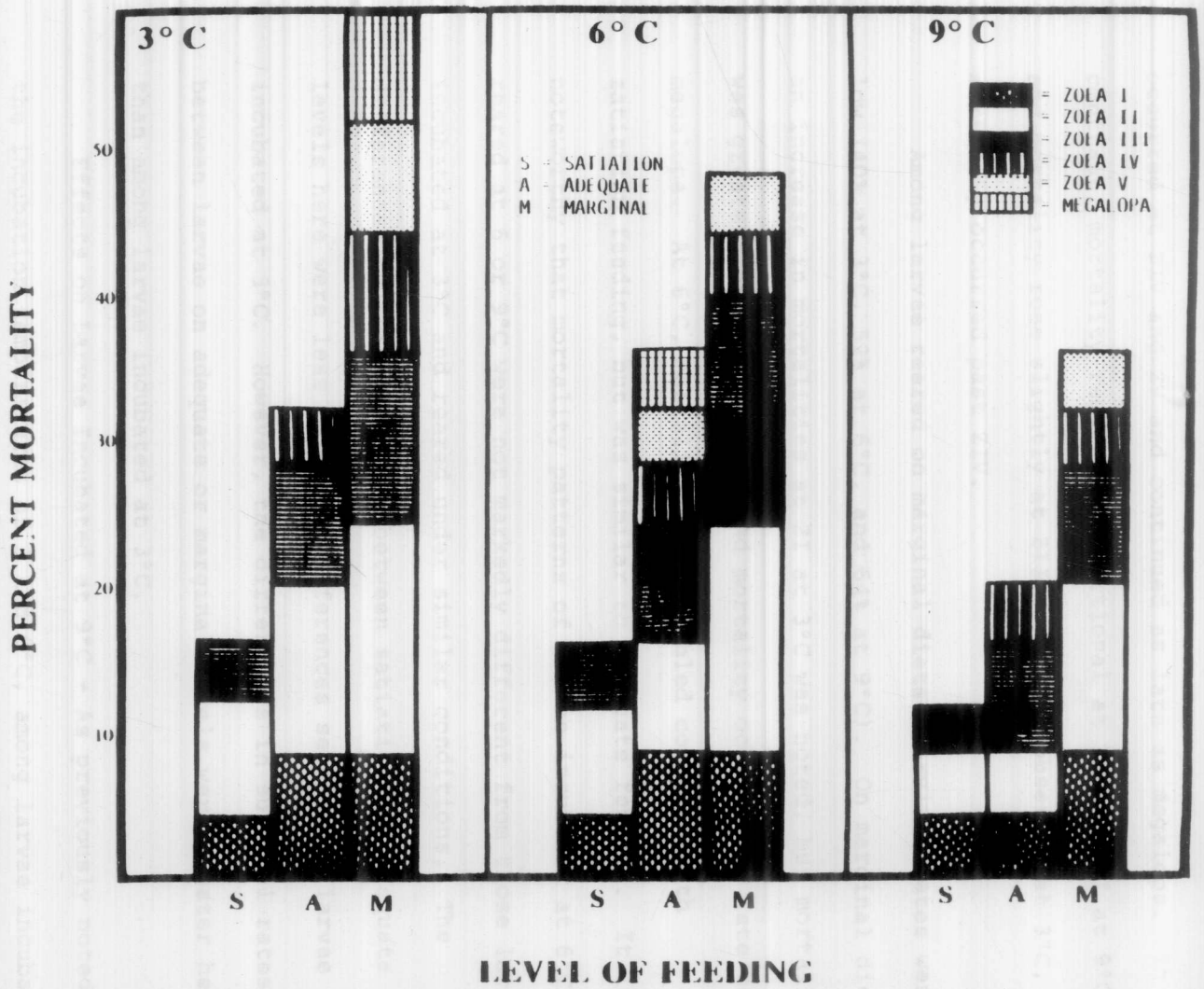


Figure 22. Mortality of Pandalus borealis larvae with an incubation temperature of 6°C and reared under different temperatures and feeding levels.

mortalities occurred past ZIV. Similarly at 6°C, mortalities rose substantially at ZI and ZII. Furthermore, mortalities occurred at ZIV and ZV and continued as late as megalopa. In contrast, mortality remained proportional at ZI and ZII at 9°C and mortality rose slightly at ZIII. As was observed at 3°C, no mortality occurred past ZIV.

Among larvae reared on marginal diets, survival rates were low (40% at 3°C, 52% at 6°C, and 64% at 9°C). On marginal diets, an increase in mortalities at ZI at 3°C was noted, but mortality was greatest at ZII and ZIII and mortality occurred as late as megalopa. At 6°C, mortality at ZI doubled compared with satiation feeding, but was similar to adequate feeding. It is noteworthy that mortality patterns of larvae incubated at 6°C and reared at 6 or 9°C were not markedly different from those larvae incubated at 3°C and reared under similar conditions. The differences in survival rates between satiation and adequate levels here were less than the differences seen among larvae incubated at 3°C. However, the differences in survival rates between larvae on adequate or marginal levels were greater here than among larvae incubated at 3°C.

Effects on Larvae Incubated at 9°C - As previously noted at the incubation temperatures of 3 and 6°C, among larvae incubated at 9°C, increasing rearing temperatures enhanced larval survival (Fig. 23). Survival rate among larvae fed ad libitum was 80% at 3 and 6°C and 88% at 9°C.

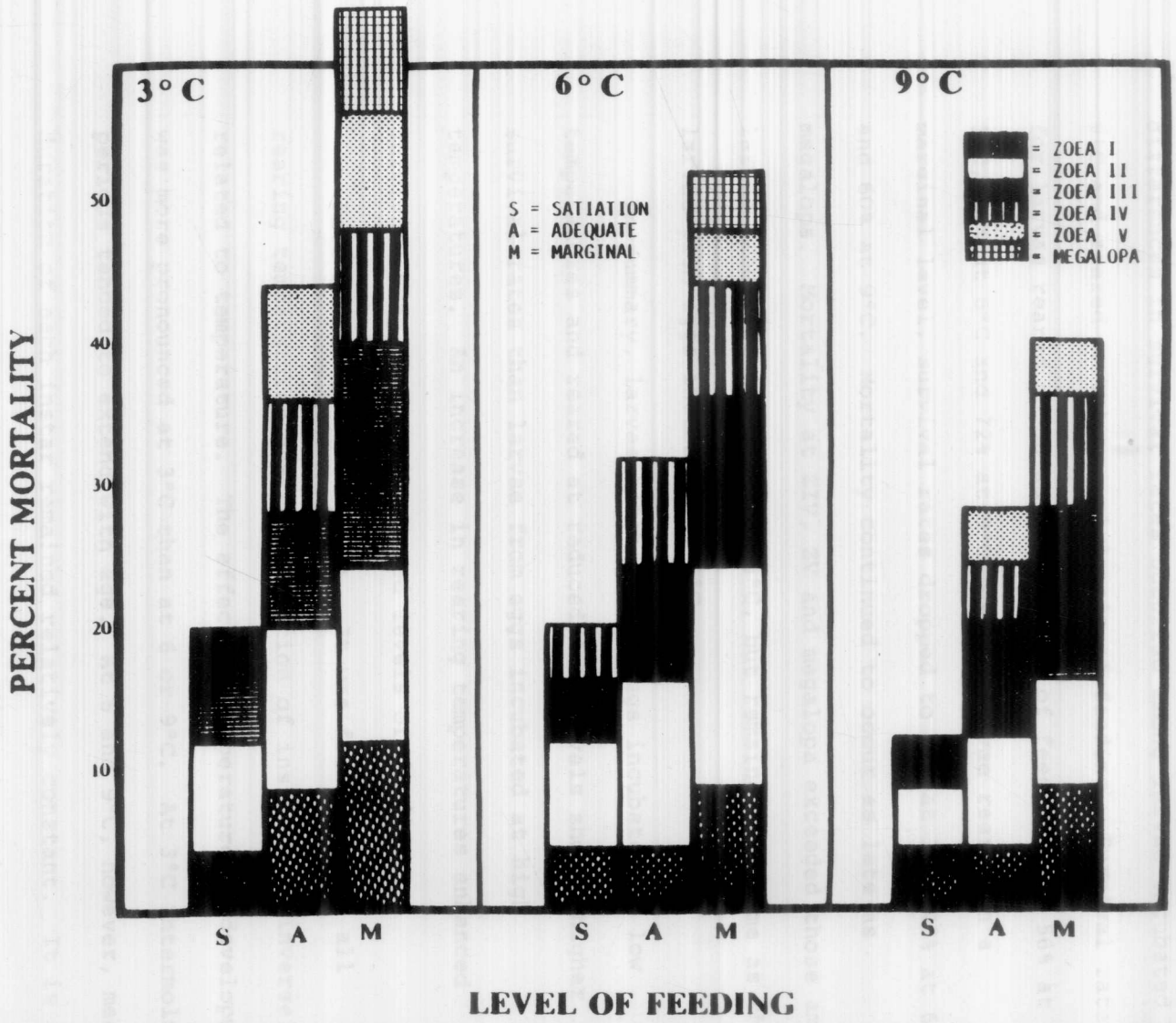


Figure 23. Mortality of Pandalus borealis larvae with an incubation temperature of 9°C and reared under different temperatures and feeding levels.

As in larvae incubated at lower temperatures, significant differences in survival rates occurred among larvae incubated at 9!C and reared on suboptimal levels of feeding. Survival rates for larvae reared on an adequate level of feeding were 56% at 3°C, 68% at 6°C and 72% at 9°C. Among larvae reared on a marginal level, survival rates dropped to 36% at 3°C, 48% at 6°C and 60% at 9°C. Mortality continued to occur as late as megalopa. Mortality at ZIV, ZV and megalopa exceeded those among larvae from eggs incubated at 3°C, but remained the same as the larvae from eggs incubated at 6°C.

In summary, larvae hatched from eggs incubated at low temperatures and reared at reduced food levels showed higher survival rates than larvae from eggs incubated at high temperatures. An increase in rearing temperatures enhanced survival among larvae on reduced levels of feeding.

Rate of Larval Development. It was found that at all rearing temperatures the mean duration of instars was inversely related to temperature. The effect of temperature on development was more pronounced at 3°C than at 6 or 9°C. At 3°C intermolt periods tended to extend with age. At 6 and 9°C, however, mean duration of each instar remained relatively constant. It is evident that molting frequency varies directly with temperature.

Reduced feeding levels resulted in widely different intermolt periods and greater variability in the number of required molts (Figs. 24-26; Table 12). All larvae fed ad

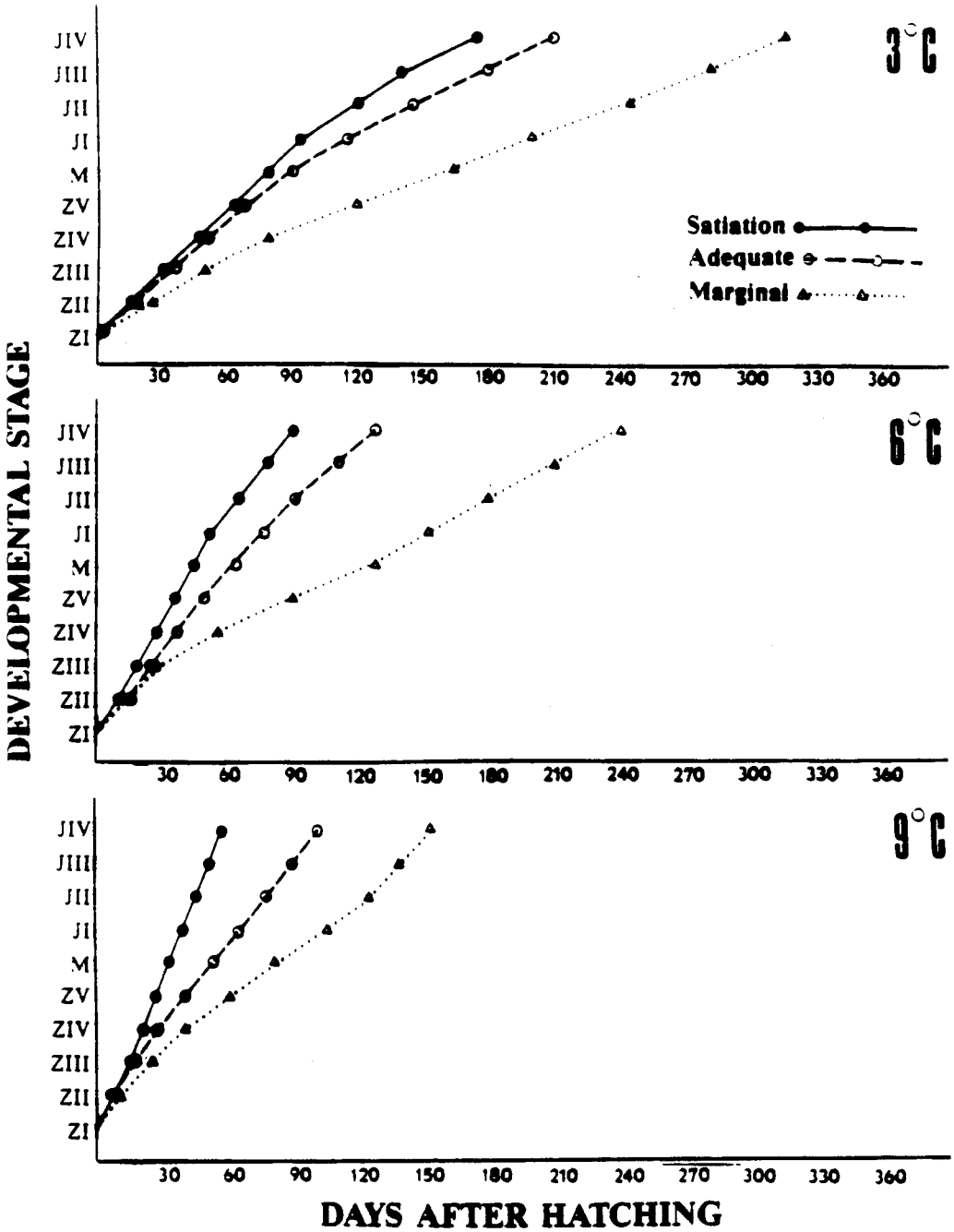


Figure 24. Rate of development of Pandalus borealis larvae with an incubation T° of 3°C and reared under different temperatures and feeding levels.

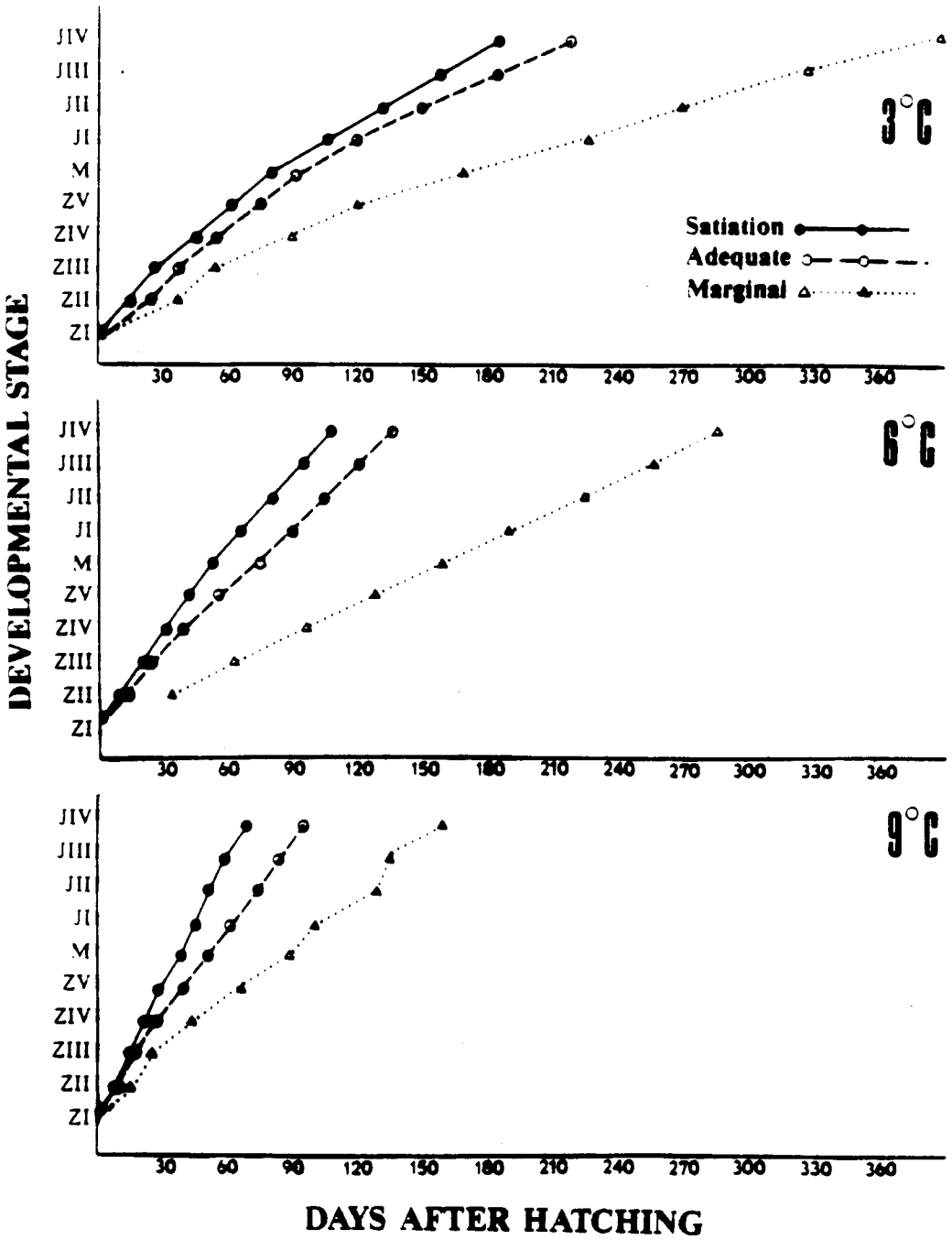


Figure 25. Rate of development of Pandalus borealis larvae with an incubation temperature of 6°C and reared under different temperatures and feeding levels.

Table 12. Comparison of the number of instars required by Pandalus borealis larvae to reach metamorphosis in relation to temperature and food availability.

Incubation Temperature (°C)	No. of Instars	Rearing Temperature (°C)								
		3			6			9		
		Food Level			Food Level			Food Level		
		S	A	M	S	A	M	S	A	M
3	6	23	12	0	23	15	0	23	17	0
	7	0	4	5	0	2	9	0	2	11
	8	0	0	3	0	0	4	0	0	6
	9	0	0	2	0	0	1	0	0	0
6	6	21	9	0	21	13	0	22	17	0
	7	0	4	4	0	2	9	0	3	10
	8	0	2	4	0	1	2	0	0	5
	9	0	0	2	0	0	2	0	0	1
9	6	18	8	0	21	12	0	22	15	0
	7	2	3	3	0	3	6	0	2	6
	8	0	3	3	0	2	3	0	1	2
	9	0	0	3	0	0	3	0	0	2

libitum passed through six molts before metamorphosis, each molt led to morphologically distinct stages. At adequate and marginal levels, larvae required an additional two or three molts to give eight or nine molts up to the time of metamorphosis. Among larvae on adequate or marginal diets, a tendency toward fewer instars and shorter intermolt periods occurred among larvae with low incubation and high rearing temperatures. The extra molts always occurred before the megalopa stage without changes in length or morphology. No larvae fed marginal levels were able to metamorphose by the 6th molt regardless of incubation and rearing temperatures. Analysis of variance showed that feeding levels had a greater effect on developmental rates than incubation temperature.

Larval Growth. Incubation temperature and level of feeding had significant effects on larval growth (Figs. 27-29). Larvae incubated at 3°C tended to reach larger sizes at metamorphosis at all rearing temperatures and feeding levels than larvae incubated at 6 or 9°C. Level of feeding had a marked effect on larval growth. Zoeae on a marginal level experienced fair growth initially but declined after the ZIII stage, suggesting that low food conditions retard larval growth. This apparent effect was reduced among larvae reared at 3°C than at 6 or 9°C. Differences between satiation and adequate diets were greatest among larvae incubated at 9°C. Unlike larvae incubated at 3 and 6°C, differences between satiation and adequate levels did not

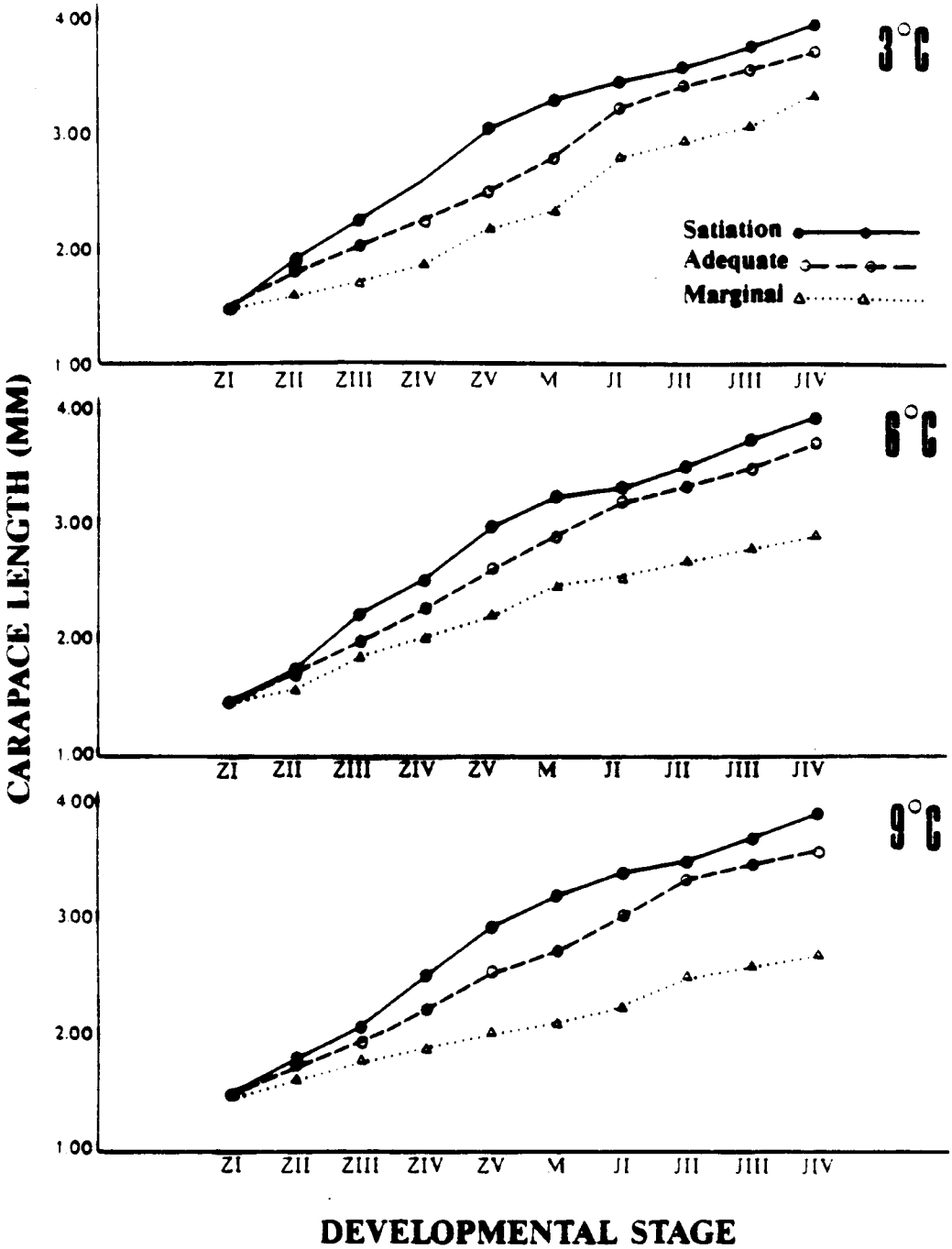


Figure 27. Growth rates of Pandalus borealis larvae with an incubation temperature of 3°C and reared under different temperatures and feeding levels.

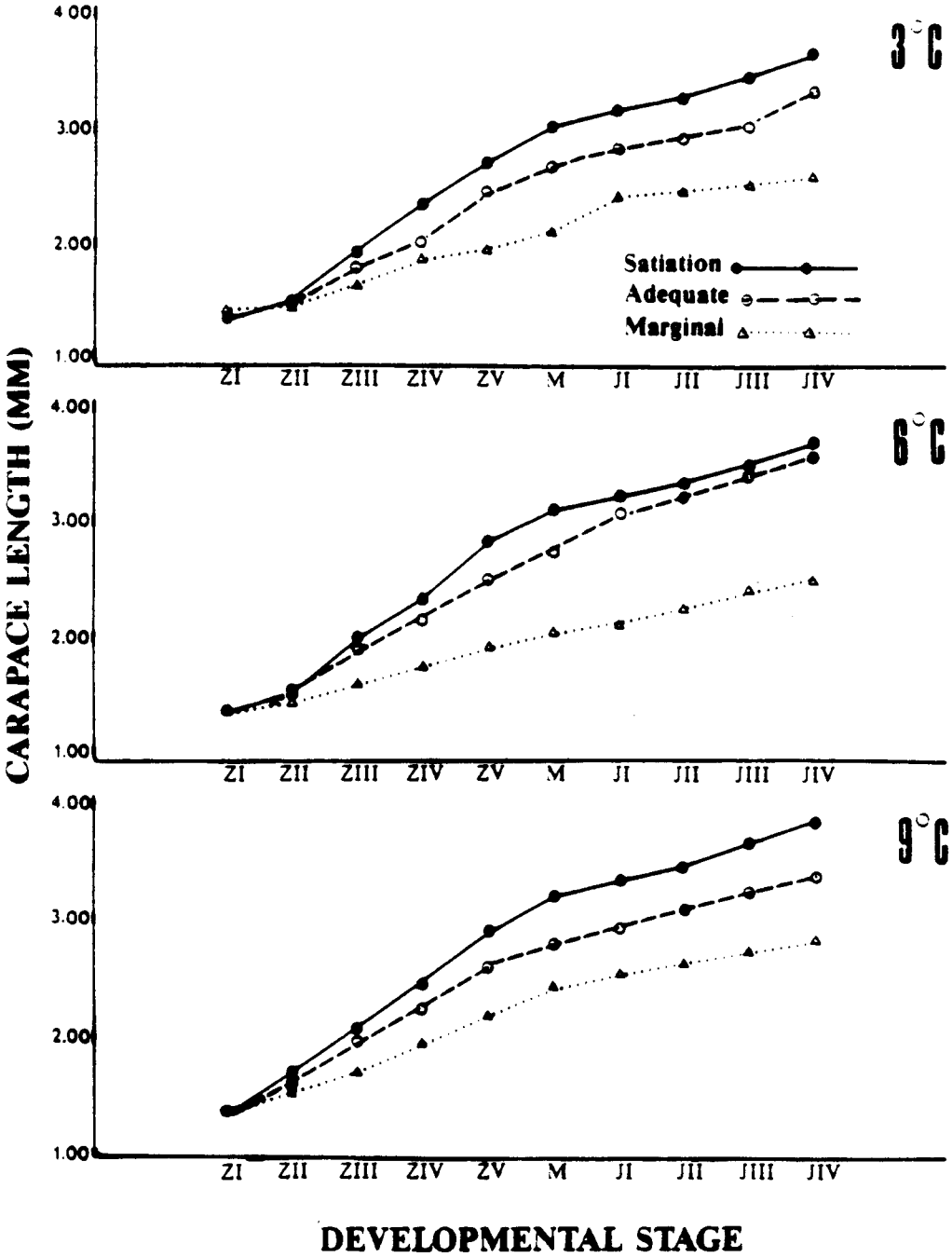


Figure 28. Growth rates of Pandalus borealis larvae with an incubation temperature of 6°C and reared under different temperatures and feeding levels.

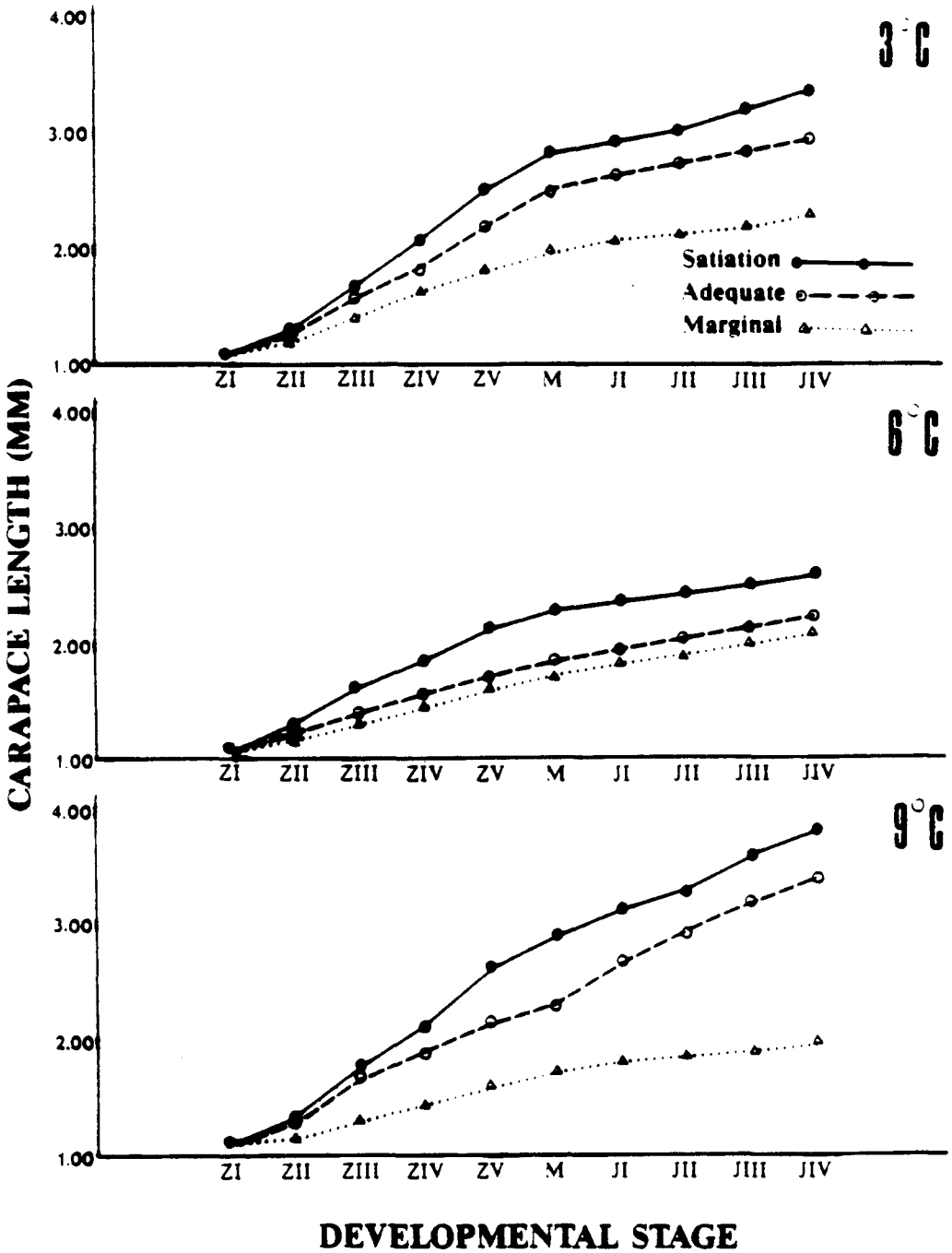


Figure 29. Growth rates of Pandalus borealis larvae with an incubation temperature of 9°C and reared under different temperatures and feeding levels.

increase with rearing temperature among larvae incubated at 9°C. Differences between adequate and marginal levels were greater among larvae incubated at 6 and 9°C than among larvae incubated at 3°C. Such differences between adequate and marginal levels tended to increase with rearing temperatures irrespective of incubation temperatures.

Figure 30 shows the relationship between larval stage and carapace length from field-sampled larvae. The curvilinear relationship among these larvae most closely resembles those laboratory reared larvae on an adequate level of feeding at the higher temperatures. Growth was most rapid during the zoeal stages, especially from ZII to ZIII, but declined markedly during metamorphosis.

Single-species algal diets. Mortality of larvae reared on different concentrations of single-species algal diets at 3 and 6°C is shown in Table 13. No single algal species supported zoeal survival to postlarvae at either temperature. None of the larvae fed the lower concentrations of single-species diatom diets of Isochrysis or Phaeodactylum reached the ZII stage at 3 or 6°C. Only 8% of the shrimp larvae reared on a low conc. of Skeletonema reached ZII at 6°C but none did at 3°C. Larvae fared better on Thalassiosira with 12% reaching ZII at 6°C but again none at 3°C. The dinoflagellates, Gonyaulax and Tetraselmis, supported greater larval survival to the ZIII stage at both temperatures. On a low concentration of Gonyaulax, 20-48% of the

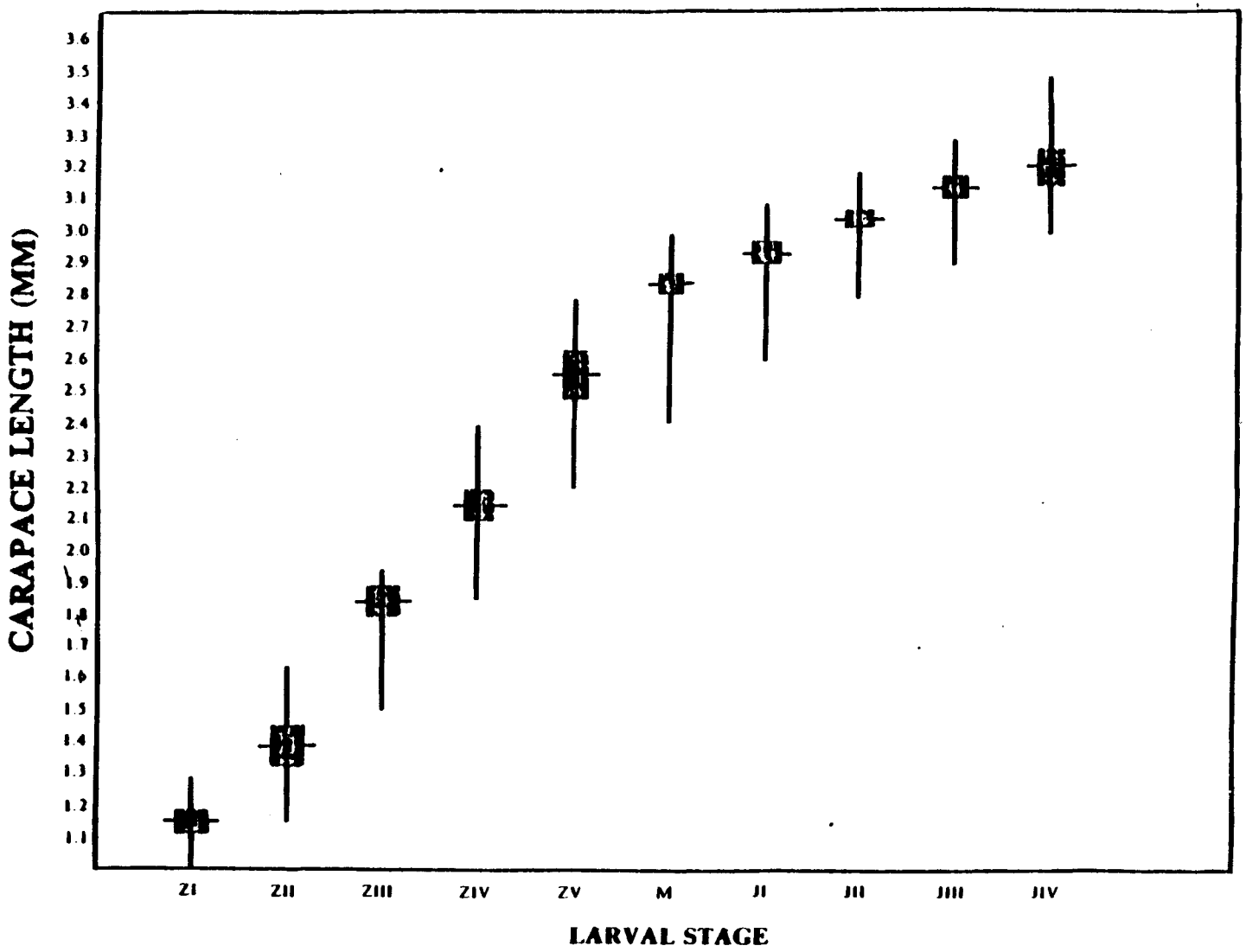


Figure 30. Growth of larval and early postlarval Pandalus borealis from Chiniak Bay, Alaska.

Table 13. Survival of Pandalus borealis larvae reared under different thermal and algal feeding regimes.

	3°C SURVIVAL			6°C SURVIVAL		
	Duration	Stage	%	Duration	Stage	%
Phytoplankton						
LOW CONCENTRATION: 500 cells per liter						
Isochrysis	17	ZI	0	20	ZI	0
Phaeodactylum	16	ZI	0	17	ZI	0
Skeletonema	20	ZI	0	23	ZII	8
Thalassiosira	22	ZI	0	27	ZII	12
Gonyaulax	35	ZIII	20	42	ZIII	48
Tetraselmis	48	ZIII	8	34	ZIII	12
HIGH CONCENTRATION: 30,000 cells per liter						
Isochrysis	27	ZII	20	22	ZII	64
Phaeodactylum	27	ZII	8	20	ZII	4
Skeletonema	30	ZII	16	30	ZIII	24
Thalassiosira	33	ZII	20	35	ZIII	32
Gonyaulax	49	ZIV	24	70	ZV	12
Tetraselmis	64	ZIII	36	60	ZIV	24

larvae survived to ZIII at 3 and 6°C, respectively. Survival was lower among Tetraselmis fed larvae. At 3°C, 8% of the larvae reached ZIII with 12% surviving to ZIII at 6°C.

Among the diatoms offered the shrimp larvae, only Skeletonema and Thalassiosira supported zoeal survival to the ZIII stage at the higher concentrations. Of the four single-species diatom diets, pink shrimp larvae fared best on Thalassiosira. In contrast, survival was poorer among larvae fed Isochrysis or Phaeodactylum with none of the larvae attaining ZIII, irrespective of temperature. Survivorship was much lower on Phaeodactylum than on Isochrysis at both 3°C and 6°C.

Survival was considerably higher among larvae reared on dinoflagellates. High concentrations of Gonyaulax supported zoeal survival to the ZIV stage at 3°C (24%) while 12% reached ZV at 6°C. At high concentrations of Tetraselmas, 36% reached ZIII at 3°C while 24% survived to ZIV at 6°C.

Mixed-species algal diets. There were no significant differences in survival between larvae fed low concentrations of mixed diatom/dinoflagellate or diatom/diatom diets but no larvae survived to ZII (Fig. 31). In only one case at 6°C (Isochrysis = Phaeodactylum = Skeletonema) did a few of the newly hatched zoeae survive to the next stage. The mixed diet composed only of the two dinoflagellates, Gonyaulax and Tetraselmis, supported greater larval survival.

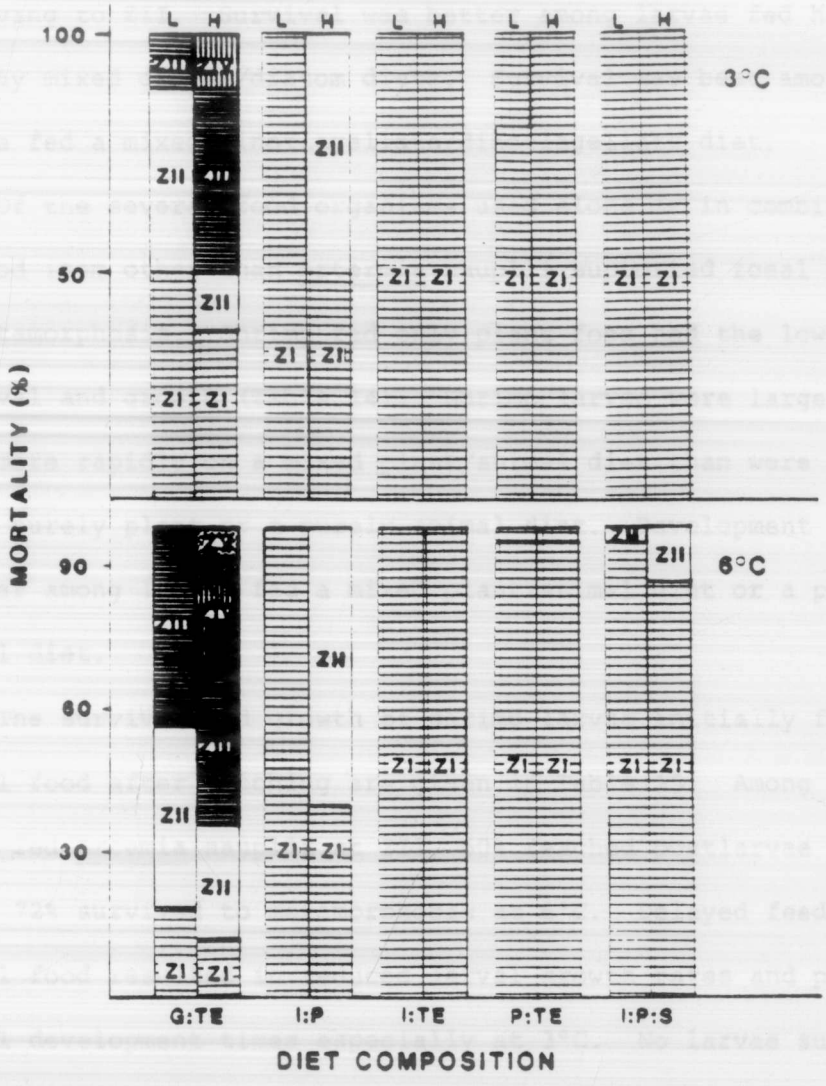


Figure 31. Percent occurrence of mortality at each developmental stage of Pandalus borealis larvae reared under different thermal and algal feeding regimes (Mixed-species diets).

Survival among larvae grown at higher concentrations of mixed diatom/dinoflagellate diets was generally low with none surviving to ZII. Survival was better among larvae fed high density mixed diatom/diatom diets. Survival was best among larvae fed a mixed dinoflagellate/dinoflagellate diet.

Of the several food organisms used alone or in combination, no food item other than Artermia nauplii supported zoeal survival to metamorphosis. Shrimp fed only plant food had the lowest survival and growth (Table 14). Shrimp larvae were larger and grew more rapidly on a mixed plant/animal diet than were larvae fed a purely plant or a purely animal diet. Development time was similar among larvae fed a mixed plant/animal diet or a purely animal diet.

The survival and growth of shrimp larvae initially fed animal food after hatching are given in Table 15. Among larvae first fed Artemia nauplii at ZII, 60% reached postlarvae at 3°C while 72% survived to metamorphosis at 6°C. Delayed feeding on animal food resulted in reduced larval growth rates and prolonged larval development times especially at 3°C. No larvae survived to metamorphosis at either temperature that had not fed on animal food until the third zoeal stage. Among these larvae 12% reached megalope at 6°C while none survived to megalopa at 3°C.

Early Starvation.

Table 14. Survival and growth of larval and postlarval Pandalus borealis reared on different plant and animal diets at 6°C.

Stage	Diet								
	Gonyaulax + Phaeodactylum + Skeletonema			Artemia salina + Gonyaulax + Phaeodactylum + Skeletonema			Artema salina		
	Age (Days)	CL (mm)	Mortality (%)	Age (Days)	CL (mm)	Mortality (%)	Age (Days)	CL (mm)	Mortality (%)
ZI	18	1.42	32	2	1.42	0	1	1.42	0
ZII	26	1.50	40	10	1.70	4	12	1.65	8
ZIII	55	1.80	28	21	2.15	4	22	2.05	4
ZIV	--	--	--	32	2.55	0	34	2.40	0
ZV	--	--	--	41	2.95	0	44	2.86	0
M	--	--	--	53	3.25	0	55	3.15	0
JI	--	--	--	64	3.36	0	68	3.22	0
JII	--	--	--	76	3.50	0	79	3.35	0
JIII	--	--	--	93	3.67	0	95	3.50	0
JIV	--	--	--	108	3.92	0	110	3.60	0

Table 15. Survival and growth of larval and postlarval Pandalus borealis in relation to the time of first feeding on animal food at 3 and 6°C.

Start of Artemia Diet (Stage)	Survival and Growth of Larvae								
	Stage	ZI	ZII	ZIII	ZIV	ZV	M	JI	JII
3°C									
ZI	Age (Days)	10	14	24	42	57	76	100	125
	CL (mm)	1.41	1.74	2.12	2.50	2.92	3.22	3.36	3.47
	Mortalities (%)	4	4	0	0	0	0	0	0
ZII	Age (Days)	23	40	63	85	110	140	162	198
	CL (mm)	1.43	1.50	1.62	1.75	1.80	1.90	1.95	2.05
	Mortalities (%)	16	12	8	4	0	0	0	0
ZIII	Age (Days)	33	52	73	95	115	--	--	--
	CL (mm)	1.43	1.48	1.55	1.65	1.70	--	--	--
	Mortalities (%)	16	32	28	16	8	--	--	--
6°									
ZI	Age (Days)	5	9	22	31	42	52	63	75
	CL (mm)	1.41	1.75	2.20	2.60	2.95	3.25	3.35	3.55
	Mortalities (%)	4	0	4	0	0	0	0	0
ZII	Age (Days)	8	20	35	60	88	114	142	174
	CL (mm)	1.42	1.50	1.65	1.78	1.85	1.96	2.08	2.20
	Mortalities (%)	12	8	4	4	0	0	0	0
ZIII	Age (Days)	15	32	50	76	110	132	--	--
	CL (mm)	1.43	1.50	1.60	1.70	1.75	1.80	--	--
	Mortalities (%)	12	28	24	12	12	12	--	--

Larval Survival - Mortality increased steadily with starvation period at all temperatures. The highest mortality rates occurred at lower temperatures.

Figures 32-34 show mortality rate at each developmental stage. After four to six days of starvation, 24-32% of the larvae did not reach metamorphosis at 3°C. A similar mortality rate of 28-36% was found at 6°C. At both temperatures, no mortality occurred following metamorphosis. Thus, there were no marked differences in survival at 3 and 6°C. However, significantly less mortality occurred at 9°C (12-20%) and in the control group (20% at 3 and 6°C; 12% at 9°C).

Larval survival rate to postlarval settling remained above 50% following six days of starvation at all temperatures. However, mortality rate was again markedly lower at 9°C (20%).

Survival rate decreased to 44 and 48% after eight days of food deprivation at 3 and 6°C, respectively.

Survival rate were below 50% after ten days of starvation at 3 and 6°C, but remained above 60% at 9°C (64%). Thus, temperature has a significant effect on survival of starved larvae. Both the number of larvae surviving and the length of time larvae were able to resist starvation were significantly reduced at the lower temperatures ($F=28.1$; $P=0.05$).

Larval Development - Development was prolonged in direct relation to length of the starvation period (Fig. 35). Significant differences in developmental rates occurred after six

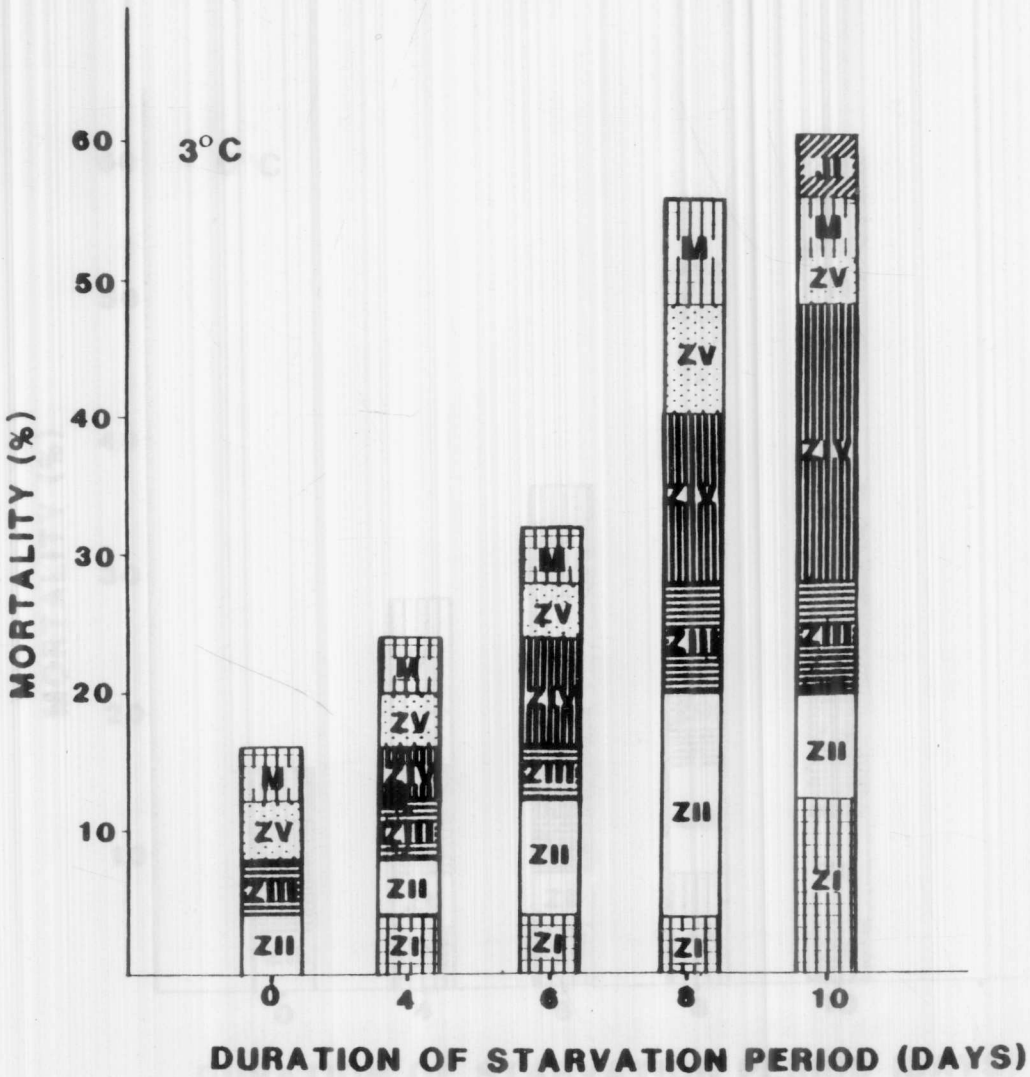


Figure 32. Percent occurrence of mortality at each developmental stage of Pandalus borealis larvae at 3°C following food deprivation.

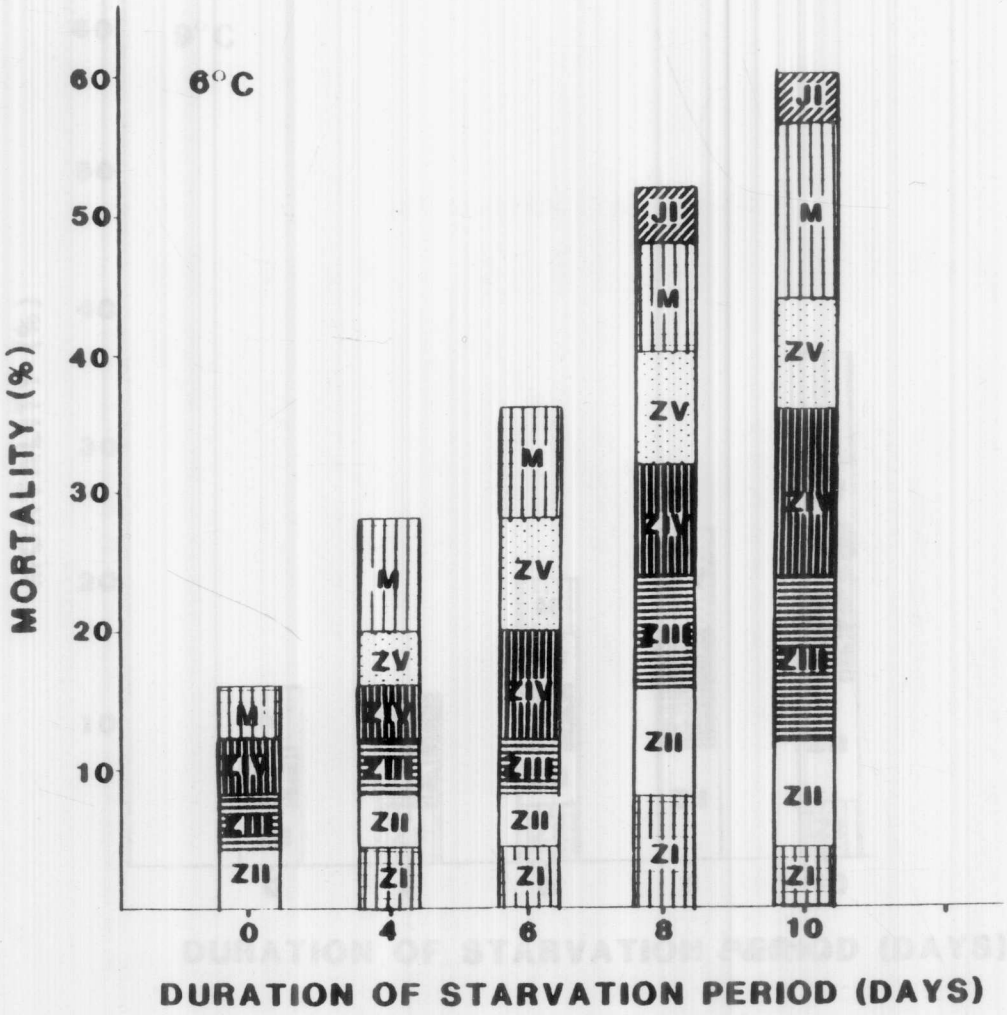


Figure 33. Percent occurrence of mortality at each developmental stage of Pandalus borealis larvae at 6°C following food deprivation.

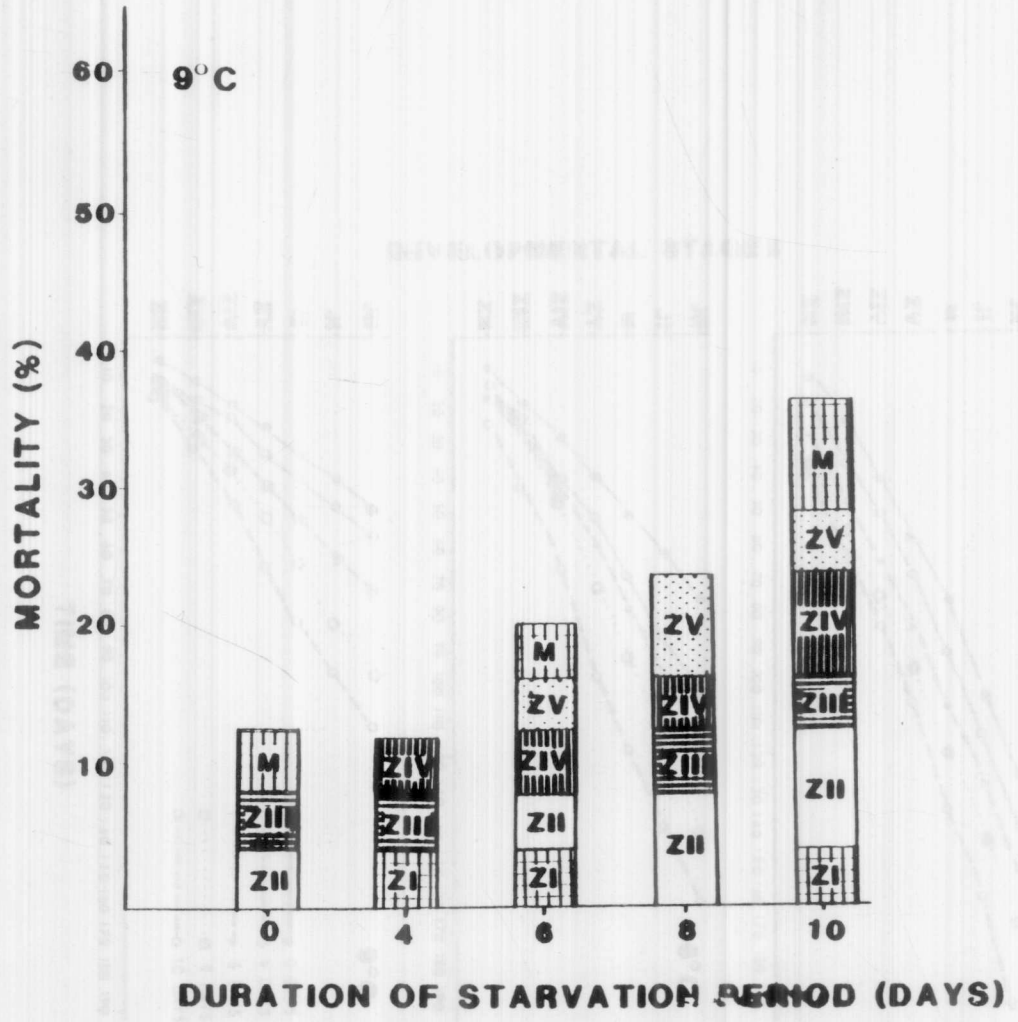


Figure 34. Percent occurrence of mortality at each developmental stage of Pandalus borealis larvae at 9°C following food deprivation.

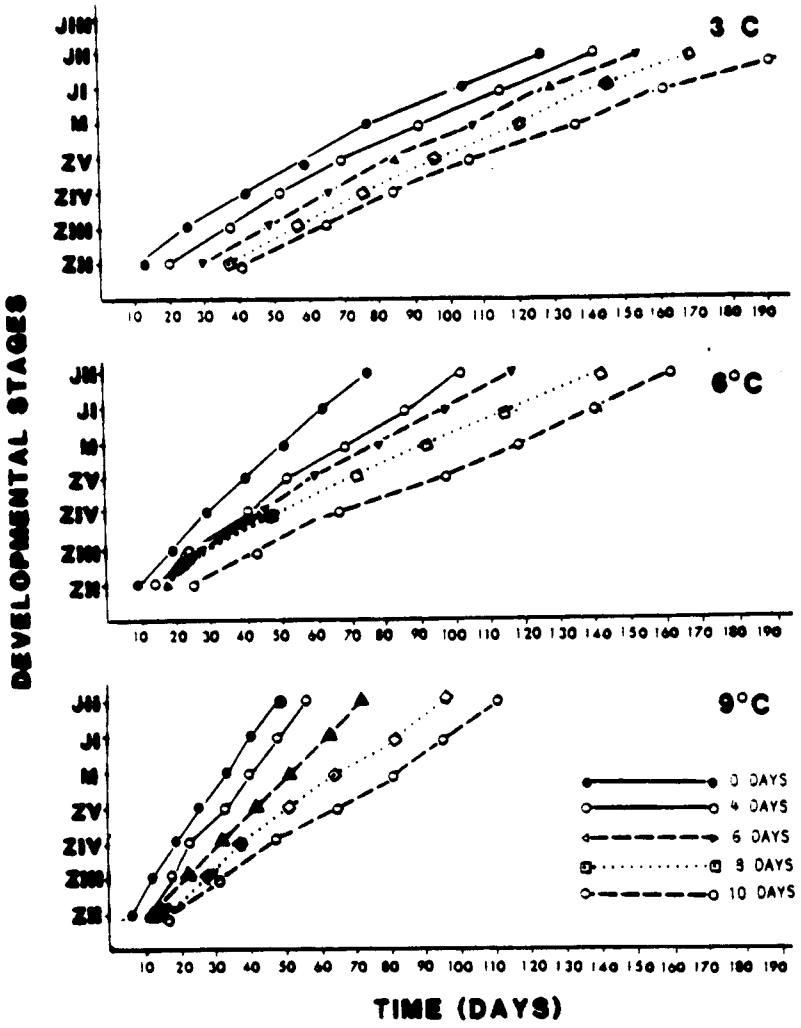


Figure 35. Pandalus borealis larval development rates in relation to temperature and duration of early starvation.

days of lack of food. Duration of larval development increased by 21% at 8°C, 49% at 6°C, and 50% at 9°C. Development was markedly prolonged after eight days of starvation at the higher temperatures, increasing by 84 and 96% at 6 and 9°C, respectively, while increasing by only 33% at 3°C. Larval development was further prolonged after ten days of lack of food by 53% at 3°C, 111% at 6°C and 125% at 9°C.

Larval Growth - Larval growth was reduced by delayed feeding (Fig. 36). Marked decreases in growth were found after six days of starvation at 3°C. At 6°C, eight days of starvation resulted in significantly lower growth. Ten days of food deprivation resulted in significantly reduced growth among larvae at 9°C. The differences in larval growth at the different temperatures were significant ($F=141.6$; $P=0.01$).

Prolonged Starvation.

Figure 37 shows the survival of starved pink shrimp larvae at 3, 6, 9, and 12°C. It was expected that survival time in starved larvae would be prolonged by low temperatures. Instead, survival time increased with temperature until 9°C. At 12°C, a marked decrease in survival time was observed. The longest survival time under starvation was 42 days at 9°C, and the shortest of 11 days at 12°C. Maximal survival times were similar at 3 and 6° of 20 and 24 days, respectively.

There were sudden large increases in mortality revealing a clear limit of starvation resistance except at 9°C. Such a

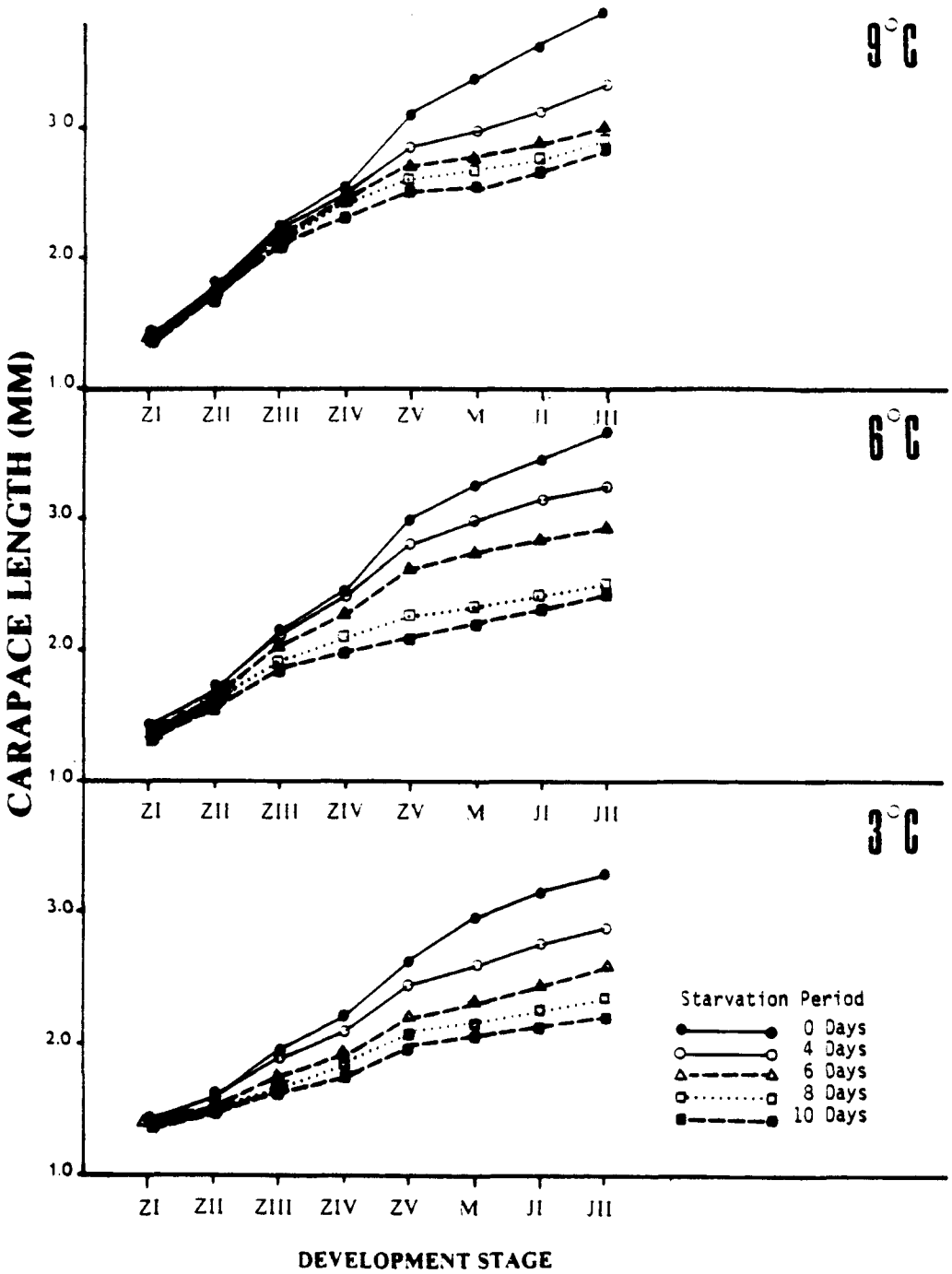


Figure 36. Pandalus borealis larval growth rates in relation to temperature and duration of early starvation.

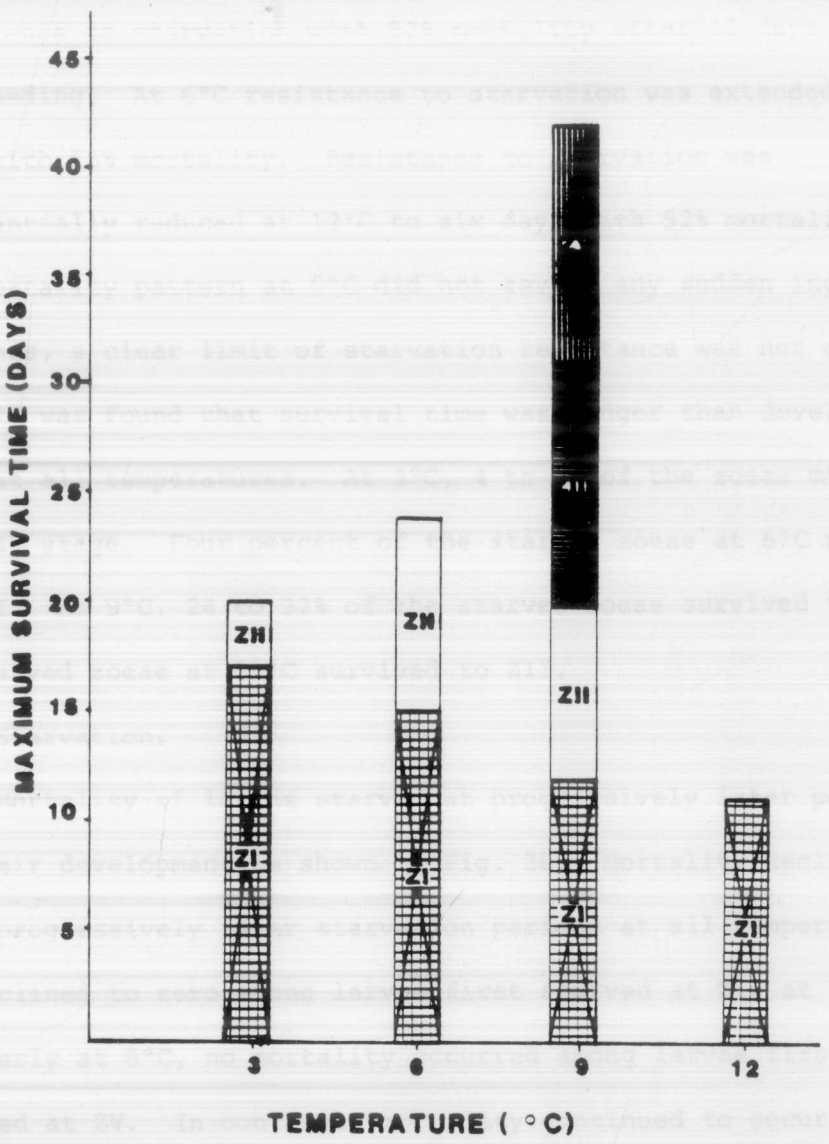


Figure 37. Maximum survival time of starved Pandalus borealis larvae in relation to temperature.

sudden increase in mortality can be regarded as a limit of starvation. At 3°C the zoeae approached the limit of their resistance to starvation with 52% mortality after 11 days of non-feeding. At 6°C resistance to starvation was extended to 13 days with 56% mortality. Resistance to starvation was substantially reduced at 12°C to six days with 52% mortality. The mortality pattern at 9°C did not reveal any sudden increases, and thus, a clear limit of starvation resistance was not evident.

It was found that survival time was longer than development time at all temperatures. At 3°C, 4 to 8% of the zoeae molted to the ZII stage. Four percent of the starved zoeae at 6°C molted to ZII. At 9°C, 24 to 32% of the starved zoeae survived to ZIV. No starved zoeae at 12°C survived to ZII.

Late Starvation.

Mortality of larvae starved at progressively later periods in their development is shown in Fig. 38. Mortality declined with progressively later starvation periods at all temperatures. It declined to zero among larvae first starved at ZIV at 9°C. Similarly at 6°C, no mortality occurred among larvae first starved at ZV. In contrast, mortality continued to occur at 3°C among larvae first starved as late as ZV. Thus, larvae are affected by starvation for longer periods at 3°C than at 6 and 9°C.

Developmental times of progressively older larvae encountering starvation after successfully molting past the first

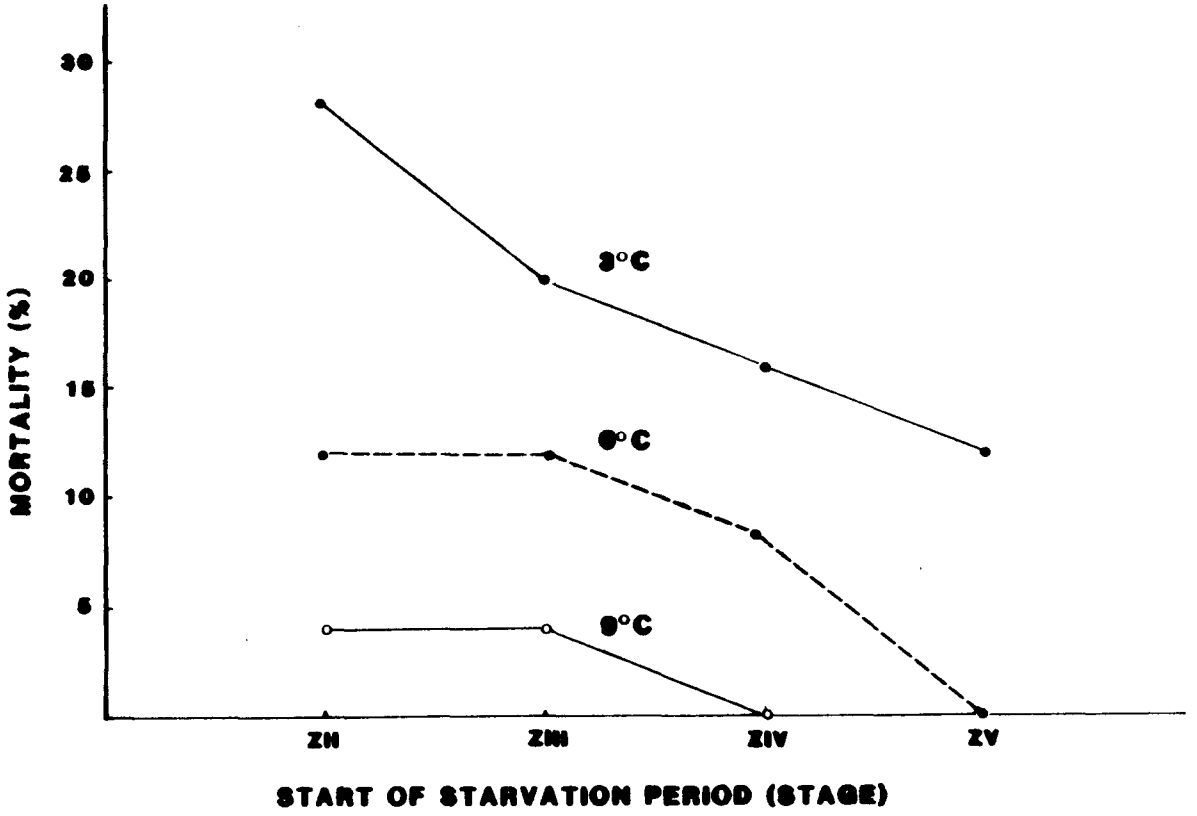


Figure 38. Mortality of Pandalus borealis larvae with different periods of late starvation and reared at different temperatures.

zoeal stage are given in Fig. 39. Development time tended to decrease as starvation was delayed at all temperatures. However, it was noted that duration of the ZV stage was markedly lengthened among larvae that were starved at ZII and reared at 3°C. Since the same trend was not seen in larvae from the other temperature and starvation combinations, it is apparent that the differences in duration of the intermolt periods was due to differences in temperature ($F=8.92$; $P=0.01$) rather than starvation ($F=1.28$; $P=0.01$).

Amount of Feeding Required for Early Survival.

Table 16 shows the survival of larvae fed the first 4, 6, 8, and 10 days after hatching and reared at 3 and 6°C. No larvae reached megalopa at 3°C. At 6°C, 4-12% of the larvae reached megalopa after eight and ten days of feeding, respectively. However, they all died soon thereafter.

Among the larvae fed for four days after hatching at 3°C, maximal survival time was 45 days with 92% of the zoeae reaching ZII. At 6°C maximal surval time was 85 days with 44% of the larvae reaching ZV.

After six days of feeding at 3°C, survival time increased by 4 days to 49 days with 12% of the larvae attaining ZIII. Similarly, survival time at 6°C increased to 91 days. However, only 24% of the larvae reach ZV.

With eight days of feeding, survival time at 3°C increased by 15 days to 64 days with 28% of the larvae reaching ZIV. At

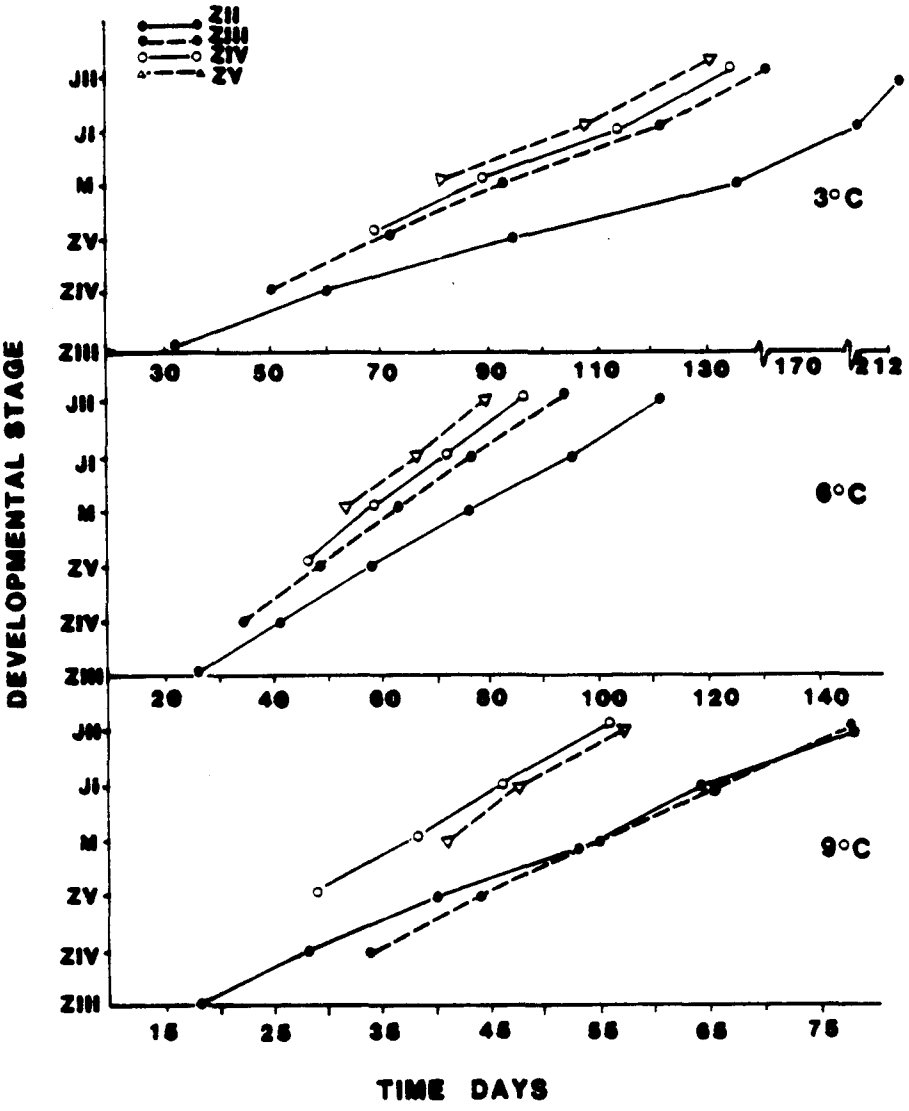


Figure 39. Developmental times of Pandalus borealis larvae in relation to temperature and late starvation.

Table 16. Survival of Pandalus borealis larvae in relation to duration of initial feeding period at 3 and 6°C.

Days of Initial Feeding	3°C SURVIVAL			6°C SURVIVAL		
	Duration (Days)	Stage	%	Duration (Days)	Stage	%
4	45	ZII	92	85	ZV	44
6	49	ZIII	12	91	ZV	24
8	64	ZIV	28	93	M	4
10	69	ZIV	20	93	M	12

6°C survival time increased by only two days to 93 days. However, the megalopa stage was attained for the first time by 4% of the larvae.

Following ten days of feeding, survival time at 3°C increased by five days to 69 days. There was a decrease in larvae reaching ZIV to 20%. No increase in survival time was observed at 6°C. Twelve percent of the larvae reached megalopa, but none survived to metamorphosis.

In summary, the differences in number of days of feeding required to complete zoeal development between temperatures was significant ($F=35.4$; $P=0.01$).

Early Starvation and Larval Feeding.

Ingestion rates of newly hatched larvae increased with prey densities and temperature, especially at 8°C (Table 17). Increases in feeding rates were smallest at prey densities between 40-60/liter and 80-100/liter, irrespective of temperature. At lower prey concentrations (20-60/liter), shrimp larvae were often unsuccessful at capturing prey at 3 and 5°C. At these temperatures, zoeae successfully consumed at least one copepod each day only at high densities of prey. At 8°C, a decrease in prey density to 60/liter adequately insured consistent capture by each zoeae of at least one prey item per day.

Zoeae that had been starved for two days after hatching showed higher ingestion rates than newly hatching zoea,

Table 17. Average daily consumption of copepods by stage 1 zoeae of Pandalus borealis after 0, 2, 4, and 6 days of starvation.

Starvation Period (Days)	Temperature (°C)	Consumption	Sample Number	Prey Density (Number l^{-1}) 20	40	60	80	100
0	3	Mean	20	0.7	1.0	1.4	2.2	2.5
		SD		0.5	0.5	0.7	1.3	1.5
		Range		0.0-1.9	0.0-2.8	0.6-3.2	1.0-4.0	1.0-4.7
	5	Mean	20	0.7	1.2	1.5	2.3	2.8
		SD		0.3	0.7	0.8	1.5	1.7
		Range		0.0-1.5	0.5-3.0	0.5-3.5	0.9-4.4	1.2-5.6
	8	Mean	20	1.2	2.1	2.5	3.1	3.6
		SD		0.3	0.8	1.1	1.4	1.9
		Range		0.0-1.8	0.5-3.1	1.2-4.1	1.6-5.4	2.5-6.1
2	3	Mean	20	0.6	1.1	1.7	2.4	2.7
		SD		0.5	0.6	1.0	1.3	1.5
		Range		0.0-1.7	0.5-3.0	0.5-3.5	1.3-4.2	1.5-4.9
	5	Mean	20	0.8	1.3	1.8	2.7	3.1
		SD		0.5	0.5	1.1	1.6	1.9
		Range		0.0-1.7	0.6-3.2	1.0-3.8	1.0-4.9	1.5-5.9
	8	Mean	20	1.5	2.5	3.0	3.7	4.2
		SD		0.6	0.7	0.9	1.2	1.6
		Range		1.1-2.5	1.5-3.5	1.8-4.0	2.5-5.5	3.0-7.5

Table 17. Continued.

Starvation Period (Days)	Temperature (°C)	Consumption	Sample Number	Prey Density (Number l^{-1}) 20	40	60	80	100
4	3	Mean	20	0.5	0.9	1.2	1.9	2.3
		SD		0.2	0.5	1.0	1.2	1.7
		Range		0.0-1.2	0.0-1.9	0.4-2.4	0.9-2.8	1.0-4.5
	5	Mean	20	0.6	1.2	1.4	2.1	2.3
		SD		0.3	0.5	0.8	1.0	1.6
		Range		0.0-1.3	0.4-2.8	0.6-3.0	1.0-3.7	1.4-4.9
	8	Mean	20	1.2	1.9	2.2	3.3	3.9
		SD		0.8	1.0	1.7	2.1	2.5
		Range		0.7-2.5	0.9-3.5	1.7-4.5	2.1-4.9	2.5-6.8
6	3	Mean	20	0.3	0.5	1.2	1.5	1.8
		SD		0.1	0.5	0.9	1.1	1.5
		Range		0.0-0.9	0.0-1.3	0.3-2.8	0.5-3.0	1.0-4.2
	5	Mean	20	0.4	0.8	1.3	1.8	2.1
		SD		0.3	0.4	0.7	0.9	1.0
		Range		0.0-1.0	0.0-1.5	0.5-3.2	1.0-3.6	1.1-4.8
	8	Mean	20	0.9	1.6	1.8	2.9	3.5
		SD		0.4	0.7	1.2	1.7	2.4
		Range		0.5-2.0	0.7-3.0	1.1-3.1	1.5-5.0	1.9-6.4

irrespective of prey density and temperature. The greatest increases in predation rates occurred at 8°C and higher prey densities. However, unlike newly hatched larvae, only at 8°C were 2-day starved larvae capable of feeding at the lowest prey density.

Ingestion rates of larvae first fed at four days of age were generally less than those for larvae fed earlier at all temperatures and prey densities. As was observed among other larvae, the greatest increases in feeding rates among 4-day starved larvae occurred at 8°C. Only at 8°C and the combination of higher prey densities of 100/liter did 4-day starved larvae show higher ingestion rates than newly hatched larvae. Four-day starved larve at 3°C required the highest prey density to satisfy their minimum metabolic requirements(Paul and Nunes 1983). At 5 and 8°C, 4-day starved larvae required the same prey densities, as newly hatched larvae to consistently capture at least one copepod daily.

While feeding rates of six-day starved larvae were lower than those for larvae first fed at day 0, overall differences in predation rates were not significant, especially at the higher prey densities. As was observed among non-starved, 2 and 4-day starved larvae, the correlated increase in ingestion rates with prey density occurred at 8°C. Ingestion rates of 6-day starved larvae at 3 and 5°C were significantly lower than at 8°C, especially at the higher prey densities. Among 6-day starved

larvae, higher temperatures clearly decreased the threshold concentration of prey organisms required for first feeding. Prey densities of 100, 80, and 60/liter were required by 6-day starved larvae at 3, 5, and 8°C, respectively. An analysis of variance revealed significant differences in feeding rates at the 1% level among shrimp larvae exposed to different prey densities F=76.3; P=0.01). While differences in feeding rates occurred among shrimp larvae with different periods of starvation, these differences were not significant (F=1.5; P=0.01).

Observations of QO_2 (Paul and Nunes 1983) and determination of the caloric value of prey items (Table 18) can be employed to estimate the minimum number of prey items that shrimp larvae must consume to survive. Ingestion rates of newly hatched and starved stage 1 zoeae reported in this study are a function of prey density and water temperature. To meet their minimum metabolic requirements from 3 to 9°C, stage 1 zoeae require up to four Acartia daily but only one Pseudocalanus (Table 18). At 3 and 5°C, both newly hatched and 2 to 4-day starved larvae require densities of Acartia in excess of zooplankton concentrations found in the Gulf of Alaska during their developmental period (Table 19). However, if water temperature is 8°C reported zooplankton densities would be sufficient to insure survival of non-starved and 2 to 4-day starved larvae. Only after six days of starvation do larvae at 8°C require prey densities in excess of those occurring in the Gulf of Alaska.

Table 18. Estimated minimum daily number of food items required by the first zoeae of Pandalus borealis at 3°C to 9°C. These estimates are based on the caloric value of food items.

Plankton	Caloric Value	Temperature (°C) 3	6	9
Artemia salina nauplii	0.00924 cal indiv^{-1} (Paffenhofer 1976)	4.8	7.0	8.1
Acartia	0.02-0.036 cal indiv^{-1} (Stickney and Perkins 1979)	1.2-2.2	1.8-3.2	2.1-3.8
Pseudocalanus	0.07 cal indiv^{-1} (Lawrence 1976)	0.6	0.9	1.1
Coscinodiscus	0.001 cal cell^{-1} (Florey 1966)	44	64	75
Skeletonema	5.247 cal mg^{-1} (Paffenhofer 1976)	114,300	174,200	204,200
Thalassiosira	5.479 cal mg^{-1} (Paffenhofer 1976)	114,700	166,900	195,600

Table 19. Prey densities of zooplankton required by Pandalus borealis stage 1 zoeae to satisfy minimum daily metablic requirements as a function of water temperature and the duration of the food deprivation period. These estimates of required prey densities were based on the caloric value of the prey item and the respiratory metabolism of one day old zoeae.

Prey Type	Starvation Period (Days)	Temperature (°C) 3	5	8
Acartia[1]	0	>100	>100	100
	2	80	>100	80
	4	>100	>100	80
		>100	>100	>100
Pseudocalanus[2]	0	60	80	60
	2	80	60	20
	4	80	80	60
	6	100	80	60

[1] 0.02 to 0.036 calories per copepod (Stickney and Perkins 1979)

[2] 0.07 calories per copepod (Lawrence 1976; Coyle, unpubl.)

In contrast to the high concentrations of Acartia required, the results presented here indicate that shrimp larvae require markedly lower prey densities where Pseudocalanus is more abundant in the plankton than Acartia. Even at temperatures as low as 3°C, Pseudocalanus-dominated zooplankton concentrations in the Gulf of Alaska would be sufficient to insure the survival of shrimp larvae regardless of length of starvation.

DISCUSSION

Planktonic shrimp larvae are exposed to environmental fluctuations caused by shifts in winds, currents and food availability. The temperature range in the Gulf of Alaska in which P. borealis larvae develop lies between 2 and 10°C (Barr 1970; U.S. Department of Commerce 1970; Niebauer 1980). The present study has shown that 9°C rearing temperatures significantly enhances larval survival. However, Kato (1974) reported that early survival rates of pink shrimp larvae were best at temperatures ranging from 4.6 to 6.7°C. On the other hand, Ohmi and Yamashita (1978) found water temperatures of 9°C to be optimal for larval survival. Similarly, Wienberg (1982) reared P. borealis larvae at temperatures from 3 to 12°C and reported highest survival rates at 9°C. My data support greater larval survival at the higher temperatures, and suggest that temperature conditions at the time of peak abundance of hatched larvae determine larval survival. Further, combined effects of low temperature, which causes prolonged development, and

dispersal may act as an important determinant of P. borealis larval survival. Although effects of temperature appear able to cause large fluctuations in survival, no conclusive evidence exists as yet to prove that variations in early mortality rates alone determine the strength of incoming year classes.

It is generally believed that in their natural environment, crustacean larvae normally pass through a variable number of developmental stages (Forster 1951; Reeve 1969). Variation in survival, number and duration of stages, and distribution of meroplanktonic invertebrate larvae has often been ascribed to temperature, acting either independently or along with other environmental factors (Costlow and Bookhout 1970, 1971; Kinne 1971). Palaemonetes microgenitor (Sollaud 1919) and Palaemonetes vulgaris (Sandifer 1973) were both found to pass through more instars at lower temperatures than at moderate temperatures. On the other hand, Ewald (1969) found that Tozeuma carolinense larvae passed through fewer instars at higher temperatures. He also reported marked differences in the number of instars among different populations of T. carolinense. In contrast, Knowlton (1965, 1970) found an increase in the number of instars with increasing temperatures for Palaemonetes vulgaris and Alpheus heterochaelis. My results agree with previous findings on the tendency toward a reduction in instars with an increase in temperature. Moreover, not only rearing temperatures, but also incubation temperatures may influence the number of instars. The

number of larval instars is important since ecdyses are considered to be critical periods involving the highest mortality in larval life (Ong 1966; Knowlton 1970; Roberts 1971). Therefore, a reduction in the number of premetamorphic molts lessens exposure to predation and may increase larval survival. Consequently, in considering the influence of molting processes on larval survival, it must be stressed that the thermal history of adult shrimp during the ovigerous period exerts a significant influence on larval viability.

P. borealis larvae were observed in the laboratory to swim with positive phototaxis. In nature, they have been found at particular depths. Larvae were found from 20 to 150 meters off the Japan Sea and the Pacific Ocean coast of Hokkaido (Kurata 1964; Abe 1968). In the Kodiak shelf region of the Gulf of Alaska, they occur between 30 to 70 meters (Kendall et. al. 1980). Thus, it is possible that P. borealis larvae actively seek food patches by regulating their vertical position in the water column. This may be accomplished by diurnal and ontogenetic vertical migrations in response to light, pressure and gravity as has been demonstrated for the larvae of Cancer magister (Jacoby 1982). Currents which might disperse the planktonic shrimp larvae are of interest since changes in thermal regime during development could negate any advantage in higher survival and growth rates at 6 to 9°C. Estimates of the temperatures encountered during the larval pelagic phase in the

Gulf of Alaska indicate that a variation from 3 to 10°C can be expected in the upper 100 meters. Surival and growth patterns in this study suggest that larvae hatched in late April encounter more favorable conditions since at this time water temperatures are generally above 5°C and food of the right quality and quantity are present and persist through the early larval stages than at any other time.

P. borealis larvae hatch in nearshore upper surface waters and the diversity of potential food items available to them is comparatively low during their early developmental stages. Should they hatch before the phytoplankton bloom occurs, they are likely to encounter microflagellates as the major component of the phytoplankton in the Gulf of Alaska (Horner et. al. 1973). As the bloom develops, microflagellates are replaced by diatoms mainly of the genera Thalassiosira, Skeletonema. Chaetoceros, Nitzchia and Rhizosolenia or by dinoflagellates predominantly of the genera Ceratium, Peridinium and Gonyaulax at densities from 5×10^5 to 3×10^6 cells l^{-1} (Horner et. al. 1973). The diatoms of the genera Isochrysis and Phaeodactylum also occur in Alaskan waters but in lower densities (K. Coyle, pers. comm.). Stickney and Perkins (1981) found that the small diatoms Skeletonema and Phaeodactylum were able to support early larval survival only at higher temperatures and in concentrations far in excess of those found in the Gulf of Maine at the time of larval hatching. However, at lower temperatures and densities similar to those

used in this study, P. borealis larvae fed a diet of small diatoms did not fare better than starved larvae. Different results were found for larvae fed larger diatoms. Stickney and Perkins (1981) reported that the large diatom, Coscinodiscus, supported larval survival at temperatures and concentrations lower than those required by shrimp larvae feeding on small diatoms. Similarly in my study, larval survival was prolonged by feeding on the larger diatom Thalassiosira. While the larvae feed on this diatoms both at sea and in the laboratory, this particular diet has been shown to be inadequate. Survival was observed in this study to be significantly higher among larvae fed the dinoflagellates Gonyaulax and Tetraselmis. From my data, it is likely that the greatest larval survival would be expected in areas where the dinoflagellate Gonyaulax occurs even at low densities and regardless of water temperature. If larval Pandalus borealis are able to survive, molt, and develop for a period of time by feeding exclusively on plant material this could be a factor in determining overall larval survival.

Mixed diets of diatoms at higher cell concentrations resulted in higher larval survival than single-species diets of either diatom at similar cell densities. Addition of dinoflagellates to a mixed diatom diet resulted in higher larval survival than a diet of only the two diatoms. In contrast, larvae reared on a mixed diet of the three diatoms, did worse than on a mixed diet of two diatoms and the single-species diet

of Skeletonema, and overall fared no better than starved larvae. Addition of the dinoflagellate Tetraselmis to the diatom Phaeodactylum resulted in poorer larval survival than for larvae grown on single-species diets of either species. This indicates that species composition is likely to be more important to larval survival and development than the total amount of phytoplankton standing stock. Morphological development is keyed to the presence of certain species that must be present at some minimum concentration sufficient to remedy deficiencies in nutritionally important components in other species.

The increased survival and accelerated development of pink shrimp larvae fed a mixed diet of plant and animal tissue seen in this study is atypical in that such diets usually result in decreased survival and retarded development among decapod larvae (Broad 1957; Chamberlain 1962; Regnault 1969). The adverse effects of mixed diets may be due to a restriction of a larva's intake of Artermia nauplii by the ingestion of algae (Broad 1957). Zimmerman (1969), however, observed greater ingestion of Artemia nauplii by Lucifer in the presence than in the absence of algae. The intake of Artemia nauplii by larval Hippolyte inermis appeared to be restricted by algae. However, survival of larvae fed a mixed diet of Phaeodactylum and Artemia nauplii, however, was greater than that of larvae fed Artemia nauplii only (Regnault 1969). While Thor floridanus successfully completed larval development to metamorphosis on a purely algal diet,

survival was significantly higher among T. floridanus larvae fed a mixed algae + Artemia nauplii diet than that seen among algae-fed and Artemia-fed larvae (Sandifer 1971). This suggests that while both T. floridanus and Pandalus borealis larvae are able to derive nourishment from both algae and Artemia nauplii, they differ in their degree of ability to utilize plant material as food. While phytoplankton can be considered to be an overall minor source of nutrition, the extent to which phytoplankton mixed with zooplankton enhances growth rates of pink shrimp larvae could be crucial in reducing predation.

A critical period early in larval development has been confirmed for the brachyuran crabs Chionoecetes bairdi (Kon 1979) and Hyas araneus (Anger and Dawirs 1981). It is also believed to occur among king crab (Paralithodes camtschatica) larvae (Kurata 1959; Paul and Paul 1980). In this study the "point-no-return" (PNR_{50}) was not reached by P. borealis larvae at 9°C even after ten days of starvation. Moreover, starvation was found to be reversible at any zoeal stage. In contrast with snow crab (Chionocetes bairdii) larval (Paul and Paul 1980), larval (P. borealis did not show a marked reduction in feeding rates at 3-5°C after six days of starvation. This suggests that P. borealis larvae are highly resistant to starvation. Thus, they may be less likely than other decapod larvae to exhibit a "critical period" more than food. Thus, it is unlikely that poor food conditions result in a high mortality of P. borealis larvae.

Anger and Dawirs (1981) found that larvae of the spider crab, Hyas araneus, did not have sufficient reserves to reach the next instar without food, irrespective of temperature. They suggested that larval development will not progress until some essential cue is provided by ingested food. It has also been suggested that since crustacean larvae do not synthesize the sterol precursors of the molting hormones they must be provided by ingested food (Whitney 1969; Gilbert and O'Connor 1970; Provasoli 1976). The presence of these substances in yolk reserves has not been reported. In contrast to crab larvae, pink shrimp larvae were able to develop to the second zoeal stage at 3 and 6°C and to the fourth zoeal stage at 9°C without feeding. In contrast, only at 12°C were the larvae unable to develop past the first zoeal stage independently of food. This suggests the presence of ecdysterone precursors in yolk reserves of P. borealis larvae but that efficient utilization is somewhat temperature dependent.

Growth rates of starved larvae were greater at 9°C than at lower temperatures. Reduction of growth will increase vulnerability to predation since predator avoidance is related to ability to sustain swimming. This ability increases rapidly with larval size. Further, it is likely that the number of potential predators declines with an increase in larval size. It is known that P. borealis larvae generally occur from March to July.

Therefore, they encounter a temperature range between 2 and 10°C. Assuming the optimal temperature range of the larval stages of P. borealis to be between 7 and 10°C based on the results of this study, it can be concluded that lower range of temperatures in the Gulf of Alaska (2-5°C) would not be favorable for P. borealis larvae.

Physical factors such as storms prevent the formation of food patches and keep prey densities below the required minimum for successful feeding by planktonic larvae. A negative correlation between recruitment and the number of stormy days has been shown for king crab larvae in Japanese waters (Ishimaru 1936). Paul et. al. (1979) suggested that if mixing from storms kept prey densities below 40 per liter, king crab (Paralithodes camtschatica), snow crab (Chionoecetes bairdi) and Pandalus borealis larvae in the Gulf of Alaska would suffer from starvation. Ingestion rates increased in this study with increasing temperature from 3 to 8°C. Larvae hatching late when water temperatures are above 5°C can thus be expected to be more successful predators than early larvae hatching at 3 to 5°C. Moreover, decrease in prey number required by starved larvae with increasing temperatures suggests that temperature may be a major factor determining early larval feeding success. Thus, adverse effects of low prey densities from storm mixing on larval feeding would be less severe on late hatching larvae when temperatures are generally above 5°C. Thus storms occurring early during the

larval hatching season would have a greater impact on larval survival then late season storms.

CHAPTER 4

GENERAL DISCUSSION

The data from this study indicate that phenotypic plasticity in response to varying environmental conditions enables shrimp populations to achieve long-term balance. This is indicated by the observation that female shrimp reduced clutch size and incubation time in warmer water and increased clutch size and incubation time in colder water.

Pandalid shrimp adopt reproductive strategies to optimize the number of offspring which can efficiently utilize available resources. Certain conservative features of the reproductive biology of pandalid shrimp lead to population stability. These include fertilization rituals, brood protection, and hermaphroditism. My results show that the pandalid shrimp, Pandalus borealis, may adopt additional tactics to maximize surviving offspring. Percentage of ovigerous females was affected by temperature during oogenesis, decreasing with increasing temperature by as much as 20-40%. Females of equal size in different areas of the Gulf of Maine produced significantly different numbers of eggs (Apollonio and Dunton 1969). The percentage of ovigerous females varied from 2 to >50% in different parts of the Gulf, and was found to be inversely related to bottom water temperatures (Apollonio and Dunton 1969). Thus, to maximize reproductive output, P. borealis undergo oogenesis at a time when temperatures are decreasing.

This study shows that under adverse conditions, i.e., increasing temperatures, P. borealis follows a reproductive strategy of maintaining somatic tissue integrity at the expense of egg production. This allows them to wait for a good year when increased size can support a larger clutch. Breeding is delayed with fewer females producing fewer but larger eggs. This is analogous to "beg-hedging" in reproductive tactics as described by Stearns (1976).

The shorter incubation period associated with increased temperature led to the production of smaller, less viable larvae in this study, and is reportedly associated with the occurrence of nonviable eggs (Apollonio and Dunton 1969; Stickney and Perkins 1979, Nunes, unpublished data). If, as demonstrated in this study, older females spawn significantly earlier when water temperatures may be low, their eggs may have a poorer chance of surviving due to increased exposure to the cold winter water temperatures. This, however, can be overcome by the longer incubation period which results in larger, more viable larvae.

If we consider variation in fecundity as a response to ecological conditions which may control the physiology of ovarian maturation, P. borealis has narrow thermal requirements for egg production. This, however, is offset by migration patterns and by varying reproductive activity in different parts of their range. P. borealis is a fall breeder in the more southerly, warmer areas (mean annual temperatures of 7-11°C; Allen 1969;

Butler 1964), a summer breeder in their more northerly areas (mean annual temperatures of 3-7°C; Rasmussen 1953; Horsted and Smidt 1956), and a year-round breeder in the coldest areas (mean annual temperatures of <3°; Abe 1977). A strategy that maximized survival of offspring might time reproduction to coincide with optimal feeding conditions for the new generation. This is likely to be the reason for the April larval hatching period in the Gulf of Alaska which would be a generally successful strategy in northern waters when temperatures are increasing.

This study demonstrates that feeding rates and survival under poor food conditions increase with increasing temperature. The studies by Lebour (1922), Stickney and Perkins (1981), and the present study point to the ability of P. borealis to utilize different food sources. I suggest that this flexibility in feeding strategies maximizes production of successful shrimp larvae. This flexibility in feeding strategies is in turn influenced by temperature.

Application to the Fishery

Well established pandalid fisheries exist along both the Pacific and Atlantic coasts of North America from California to Alaska and from Maine to Newfoundland, respectively. In addition, pandalid fisheries occur off the west coast of Greenland, in the Norwegian Sea and North Sea, in the northwestern Pacific Ocean where they are fished by Japan, Korea,

and the Soviet Union, and in the southern hemisphere as well off Chile and India (Fox 1972).

Eight species of pandalid shrimp occur in Alaska's shrimp fisheries (Fig. 1), but only five are of commercial importance. The northern pink shrimp, Pandalus borealis Krøyer, comprises at least 85 percent of all trawl-caught shrimp from the Gulf of Alaska, Aleutian Islands and eastern Bering Sea. P. platyceros Brandt (spot shrimp) and P. hypsinotus Brandt (coonstripe shrimp) have at times supported small pot fisheries in the central and eastern Gulf regions. P. goniurus Stimpson (humpy shrimp) and Pandalopsis dispar Rathbun (sidestripe shrimp) are at times dominant in commercial trawl catches from specific areas, and occasionally support small fisheries. Other pandalids, P. danae Stimpson (dock shrimp), P. monagui tridens Rathbun, P. jordani Rathbun (ocean shrimp) occur in catches to a minor extent (Gaffney 1977).

Commercial exploitation of pandalid shrimp began in southeastern Alaska near Petersburg in 1915 (Harry 1963). The fishery gradually expanded from half a million pounds in the 1920s to three million pounds in the mid-1950s. Introduction of the mechanical peeler in 1957 combined with increased consumer demand, reduced production of shrimp in the Gulf of Mexico, and discovery of new harvestable populations in the western part of the Gulf of Alaska contributed to a marked expansion of the Alaskan shrimp industry. By 1959 the total Alaskan shrimp catch

increased to more than 13 million pounds with the Kodiak District accounting for approximately 2.9 million pounds (Jackson 1968). Statewide landings of P. borealis steadily increased from about eight million in 1958 to over 110 million pounds in 1975, making the Alaskan shrimp fishery one of the world's largest (Gaffney 1977). Catch data for 1977-82, however, show a drastic decline to less than 25 million pounds since this period (Jackson et. al. 1983).

The tendency of shrimp stocks to rise and fall in a cyclic manner poses a major difficulty in the management of pandalid shrimp fisheries on a worldwide basis. The Kodiak Island pandalid shrimp fishery peaked at about 75 million pounds in 1971-72 followed by a drastic decline to 22-25 million pounds in 1977-78. The 1979-80 harvest continued a 3-year decline, and is the lowest since 1969 (Jackson 1980). The fishery for P. borealis in the Gulf of Maine was good to excellent from 1938 to 1945 but deteriorated thereafter until the mid-1950s. However, it returned to former levels or better in the 1960s and 1970s (Anthony and Clark 1978). The Danish fishery for P. borealis began in 1931 and was based on the stocks in the Kattegat and Skagerrak. Later is expanded into the North Sea increasing steadily to a peak in 1969. A failure of the fishery off Greenland occurred from 1948 to 1953 (Horsted and Smidt 1953). A sudden fall in the Fladen Ground fishery occurred in 1973 that has been followed by a steady rise since 1975 (Smidt 1979). The

pandalid shrimp fisheries off the coast of Washington and Oregon have also registered increases and decreases in a similar manner (Balsiger 1979). However, the Pribilof Island shrimp fishery in the Bering Sea has produced no significant harvests since its decline in 1971.

This study provides useful information for management of the fishery by demonstrating that temperature can trigger fluctuations in the commercial catch from 5-50% through its effects on rates of reproduction and larval 6°C, survival, and thereby population size. In warm water areas averaging 6°C, temperature exerts its main influence on reproduction, causing fecundity to vary by as much as 50%. While in colder areas average 3°C, fecundity and larval survival can vary with temperature by as much as 20 and 40%, respectively. Use of the information derived here requires monitoring temperature in the major fishery areas to detect changes in abundance of ovigerous females, egg number and larval survival. Changes in these parameters are valuable indicators of stock condition when combined with abundance surveys and fishing intensity estimates.

Suggested Areas for Future Study

In contrast to some decapod and fish larvae, Hjort's concept of a "critical period" (1926) is not applicable to P. borealis larvae at the temperature range encountered during their development. Since a temporary lack of food does not appear to be as effective as temperature in controlling the survival of P.

borealis larvae, other major sources of mortality must be sought in the effects of predation and competition. The widespread distribution and high abundance of P. borealis in the North Pacific make it a food source for larger organisms. P. borealis is a regular component in the diet of cod, pollock, halibut and other bottomfish, but the impact of predation on the recruitment process remains poorly understood.

Another area of interest in the recruitment process is the marked variability in the sexual transition of pandalid shrimp. Among Pandalus jordani off the coast of California, the proportion of shrimp acting as primiparous females varies from 13-63% from year to year. It is commonly accepted that sex reversal in pandalid shrimp is related to the attainment of some critical size (Rasmussen 1953; Fox 1972). The variability in the time of onset of sexual maturity and sexual transition of P. borealis is believed to be due to annual fluctuations in thermal conditions or food supply in the locale inhabited by the shrimp and its effects on growth rates (Rasmussen 1953; Jensen 1965; 1967). Charnov et. al. (1978), however, proposed that the fluctuations in sex reversal in P. jordani off the California coast was not related to changes in growth rates but rather to fluctuations in age distribution. These authors suggested that the predicted age of sex reversal was most sensitive to adult mortality rates and not to growth rates. Reviewing catch data on P. borealis from the Skagerak fishery, Charnov (1981) concluded

that higher adult mortality rates selected for a shorter male phase. That work contended that P. borealis responds to heavy fishing exploitation by lowering the age of sex reversal. Available catch data on P. borealis from the Gulf of Alaska suggest that heavy fishing exploitation and increased predation by cod on pink shrimp have caused an earlier age of sex reversal and a decrease in the average size of pink shrimp in the commercial catch.

CHAPTER 5

SUMMARY

1. The effects of water temperature on aspects of the reproductive and larval biology of the northern pink shrimp, Pandalus borealis Krøyer, were examined for clues as to what role temperature plays in the abundance fluctuations of this species in Alaskan waters. Emphasis was placed on the temperature requirements for ovarian maturation, optimum egg production, lowest incidence of unproductive spawning, embryonic development, and maximal larval survival and growth.

2. To test the hypothesis that low annual water temperatures result in poor recruitment, the larval biology of P. borealis was examined. The extent to which temperature modifies metabolic requirements, predation rates, and starvation resistance of larvae were of particular concern. The relationship of temperature and food availability to larval survival, development, and growth was also examined. Another objective of this study was to determine if the larvae can complete their pelagic phase of development on naturally occurring phytoplankton.

3. It was found that ovarian maturation is temperature-dependent in a cold year, spawning in Alaskan waters will be delayed by a month and result in a 10% reduction in the number of spawning females. In a warm year, shrimp may delay spawning by 4-6 weeks

and experience as much as 20% reduction in the number of breeding females.

4. Optimum temperatures for the reproductive processes varied within a range of 3°C. Maximum percentage of females in the population that reproduced successfully occurred at 6°C, declining by 8-10% at 3°C with a further decrease of 20-22% at 9°C. Shrimp at 3°C produced the greatest number of eggs but egg survival was highest at 6°C. Shrimp at 9°C produced the fewest but the largest eggs. Shrimp at 3°C had the highest larval hatching success and produced the largest larvae. Larvae from eggs incubated at 3°C were more viable than larvae from eggs incubated at higher temperatures. The greatest variability in egg production occurred among smaller shrimp, especially at higher temperatures. It is inferred that in the natural environment, total population fecundity will vary with temperature by as much as 20%.

5. There are three potential effects of the thermal history of adult shrimp during the ovigerous period on the larvae they produce. A reduction in the number of premetamorphic molts and in the duration of intermolt periods, and an increase in final size at metamorphosis tend to increase survival among larvae incubated at low temperatures.

6. Larval survival was significantly greater at 9°C than at 3 or 6°C. The effect of temperature on larval developmental rate was more pronounced at 3°C than at 6 or 9°C. However, rearing

temperatures had no significant effect on final size at postlarval settling. In contrast, incubation temperatures and food availability had significant effects on larval growth. Larvae incubated at low temperatures reached larger sizes at metamorphosis irrespective of rearing temperature and feeding levels than larvae incubated at higher temperatures.

7. The adequacy of the diatom and dinoflagellate species commonly found in Alaskan waters at the time of larval hatching was investigated. Phytoplankton used included Gonyaulax, Isochrysis galbana, Phaeodactylum tricornutum, Skeletonema costatum, Thalassiosira, and Tetraselmis. Diatom-fed larvae did not fare significantly better than starved larvae under simulated conditions of temperature and phytoplankton concentrations found under bloom conditions. However, larvae fed dinoflagellates fared markedly better than diatom-fed larvae. At temperatures and phytoplankton concentrations occurring at the time of spring bloom, larvae feeding on the dinoflagellate, Gonyaulax, are able to complete the zoeal portion of their development. However, larvae were found to require animal tissue by the second zoeal stage in order to complete development to metamorphosis.

8. The longest survival time of larvae under starvation of 42 days was observed at 9°C with 24-32% of the larvae surviving to ZIV. Larvae were found to remain particularly sensitive to starvation only during the ZI-ZIII stages. Prey densities required to insure successful first feeding by starved larvae

decreased with an increase in temperature. Moreover, the amount of food required by larvae to complete development was significantly reduced at higher temperatures. It was estimated that larvae at higher temperatures require a total of 10 days of feeding to complete development. It is concluded that a high mortality of pink shrimp larvae will not be caused by poor food conditions at sea.

APPENDIX

Table 20. Mean monthly ambient temperatures of incoming seawater at the Seward Marine Center Laboratory.

Monthly/Year	Mean Monthly T°C	Range
January 1978	6.0	5.5 - 6.3
February	5.5	5 - 6
March	5.6	5 - 6
April	5.0	5 - 5.5
May	6.0	5 - 7
June	6.5	6 - 7
July	6.1	6 - 6.5
August	6.5	6.5 - 6.6
September	7.4	6.5 - 9.5
October	9.6	8.0 - 10.5
November	9.1	8.7 - 9.5
December	8.3	7.5 - 8.7
Annual Mean T°C for 1978:	6.8	5.0 - 10.5
January 1979	6.9	6.2 - 7.5
February	4.8	3.8 - 6.5
March	4.2	3.3 - 4.9
April	4.3	3.9 - 4.7
May	4.7	4.4 - 5.0
June	5.2	4.8 - 5.5
July	6.2	6.0 - 6.7
August	6.8	6.0 - 7.1
September	7.7	7.0 - 8.2
October	8.9	8.0 - 9.0
November	9.5	9 - 10
December	7.1	6.6 - 7.9
Annual Mean T°C for 1979:	6.4	3.3 - 10.0
January 1980	6.1	5.2 - 7.8
February	4.9	4.5 - 6.0
March	4.8	3.9 - 5.2
April	4.3	3.9 - 4.7
May	4.4	4.3 - 4.8
June	5.7	4.5 - 6.0
July	6.0	4.9 - 6.5
August	6.6	6.0 - 7.4
September	8.8	7.9 - 9.6
October	9.1	8.3 - 9.7
November	8.5	7.5 - 8.5
December	6.8	4.9 - 8.0
Annual Mean T°C for 1980:	6.3	3.9 - 9.7

Table 20. Continued.

January 1981	5.3	4.9 - 5.7
February	5.3	5.2 - 5.5
March	5.0	3.7 - 6.0
April	5.8	5.4 - 6.2
May	5.9	5.6 - 6.2
June	6.2	5.4 - 6.8
July	7.2	6.1 - 8.7
August	7.2	5.9 - 9.3
September	8.3	7.0 - 10.3
October	8.7	7.7 - 9.4
November	8.0	6.8 - 8.6
December	7.3	6.0 - 8.3
Annual Mean T°C for 1981:	6.7	3.7 - 10.3
January 1982	5.9	4.6 - 7.4
February	5.1	4.0 - 6.8
March	4.0	3.5 - 4.8
April	4.1	3.9 - 4.6
May	4.6.	4.1 - 5.4
June	5.3	4.4 - 6.2

Table 21. Depth and seasonal distribution of temperature and salinity in Resurrection Bay, Alaska 59°50'N; 149°30'W (T.R. Royer, pers. comm.).

Date	Item	Depth (Meters)											
		0	5	10	15	20	30	50	75	100	150	200	250
Jan.22,1975	T°C	4.03	4.04	4.05	4.05	4.04	4.09	4.32	4.64	4.97	5.45	5.98	6.02
	S‰	30.99	30.99	31.00	31.01	31.01	31.04	31.15	31.30	31.64	32.05	32.51	32.85
Feb.2,1979	T°C	4.15	4.14	4.16	4.14	4.15	4.17	4.19	4.27	4.29	5.59	5.77	5.88
	S‰	31.47	31.48	31.44	31.47	31.48	31.48	31.48	31.45	31.45	32.18	32.61	32.91
Feb.13,1975	T°C	3.43	3.44	3.44	3.45	3.45	3.46	3.59	3.75	3.89	3.79	5.58	
	S‰	31.42	31.42	31.42	31.42	31.42	31.42	31.46	31.49	31.53	31.54	32.34	
Feb.16,1978	T°C	3.98	3.98	3.98	4.04	4.15	4.22	4.27	4.35	4.52	4.64	4.78	5.02
	S‰	31.30	31.32	31.31	31.35	31.45	31.46	31.49	31.55	31.66	31.89	31.98	32.11
Feb.17,1979	T°C	3.74	3.74	3.74	3.74	3.75	3.74	3.73	3.68	4.23	5.17	5.75	5.82
	S‰	31.51	31.50	31.51	31.51	31.51	31.51	31.53	31.59	31.67	31.90	32.50	32.90
Mar.2,1976	T°C	2.84	2.86	2.84	2.79	2.76	2.76	2.74	2.74	2.87	3.86	4.37	4.64
	S‰	31.60	31.60	31.61	31.61	31.61	31.61	31.62	31.62	31.64	32.07	32.30	32.63
Mar.3,1971	T°C	1.97	1.94	1.87	1.87	1.88	1.89	1.95	1.99	2.01	2.08	2.12	
	S‰	32.30	32.29	33.32	32.33	32.34	32.35	32.38	32.40	32.42	32.50	32.71	
Mar.22,1975	T°C	2.84	2.84	2.87	2.88	2.89	2.91	2.92	3.04	3.52	3.71	4.34	4.95
	S‰	31.47	31.47	31.49	31.47	31.49	31.48	31.50	31.54	31.75	31.98	32.23	32.58
Mar.28,1974	T°C	2.91	2.92	2.82	2.81	2.82	2.75	2.70	2.58	2.71	3.27	4.03	4.67
	S‰	31.59	31.66	31.70	31.73	31.74	31.76	31.79	31.83	31.93	32.12	32.46	33.87

Table 21. Continued.

Date	Item	Depth (Meters)											
		0	5	10	15	20	30	50	75	100	150	200	250
Mar.31,1977	T°C	4.26	4.26	4.26	4.27	4.27	4.27	4.51	5.19	5.70	6.07	5.77	5.75
	S‰	30.72	30.72	30.69	30.71	30.70	30.71	30.85	31.27	31.61	32.40	32.79	32.83
Apr.3,1979	T°C	3.76	3.77	3.64	3.60	3.63	3.67	3.79	3.86	3.64	4.10	4.32	4.61
	S‰	31.43	31.43	31.42	31.47	31.48	31.49	31.67	31.91	32.02	32.15	32.23	32.34
Apr.4,1972	T°C	1.79	1.79	1.78	1.78	1.77	1.76	1.76	1.85	1.86	2.22	2.50	2.94
	S‰	31.91	31.94	31.95	31.96	31.97	31.97	32.00	32.09	32.10	32.36	32.43	32.61
Apr.11,1975	T°C	3.23	3.11	3.13	3.20	3.25	3.26	3.27	3.27	3.32	3.60	3.81	4.45
	S‰	31.42	31.45	31.48	31.57	31.59	31.59	31.61	31.63	31.71	31.95	32.05	32.54
Apr.20,1976	T°C	3.15	3.19	3.23	3.10	3.13	3.34	3.39	3.40	3.38	3.65	3.79	3.89
	S‰	31.53	31.59	31.59	31.63	31.69	31.73	31.78	31.78	31.80	32.03	32.13	32.16
Apr.27,1982	T°C	4.06	4.07	4.03	4.08	4.12	4.10	4.14	4.09	4.07	4.04	4.17	5.18
	S‰	31.35	31.36	31.57	31.65	31.68	31.69	31.72	31.75	31.79	31.89	31.99	32.64
May4,1978	T°C	6.68	5.87	5.63	5.56	5.29	4.99	4.96	4.80	5.13	5.14	5.23	5.21
	S‰	31.24	31.23	31.28	31.28	31.31	31.44	31.50	31.64	31.90	32.19	32.50	32.72
May7,1975	T°C	4.54	4.54	4.55	4.40	3.94	3.79	3.62	3.57	3.73	4.23	4.69	
	S‰	31.18	31.18	31.18	31.19	31.43	31.51	31.53	31.72	31.84	32.26	32.89	
May15,1982	T°C	5.99	5.50	5.01	4.95	4.63	4.48	4.39	3.99	4.04	4.12	4.74	5.07
	S‰	30.61	31.36	31.49	31.55	31.58	31.64	31.71	31.78	31.83	31.98	32.34	32.63

Table 21. Continued.

Date	Item	Depth (Meters)											
		0	5	10	15	20	30	50	75	100	150	200	250
May17,1979	T°C	6.19	6.17	6.09	6.02	6.00	5.77	5.61	4.62	4.08	4.41	4.93	4.97
	S‰	31.14	31.16	31.18	31.24	31.24	31.35	31.62	31.77	31.85	32.25	32.77	32.92
June3,1975	T°C	7.51	6.45	5.67	5.55	5.52	5.25	4.93	4.02	3.92	4.49	4.63	4.67
	S‰	29.82	30.75	31.23	31.29	31.32	31.48	31.61	31.62	31.83	32.51	32.88	32.95
June10,1974	T°C	11.14	8.36	7.84	8.18	7.69	5.79	4.43	3.83	4.36	4.12	4.38	4.63
	S‰	25.43	30.98	31.28	31.68	31.76	31.61	31.79	31.96	32.12	32.31	32.55	32.66
June11,1980	T°C	10.03	7.47	6.72	6.91	6.67	6.66	5.45	5.34	5.24	5.51	5.71	5.70
	S‰	27.72	30.47	30.65	30.92	31.02	31.28	31.54	31.80	31.98	32.33	32.51	32.58
June11,1982	T°C	8.60	8.57	8.06	7.17	6.60	5.71	5.00	4.94	4.34	4.64	5.03	5.13
	S‰	29.24	29.70	30.75	31.39	31.53	31.66	31.76	31.83	31.87	32.18	32.47	32.57
June21,1976	T°C	10.75	8.83	8.03	7.81	7.78	7.39	7.43	4.88	4.79	4.93	4.65	4.62
	S‰	28.51	30.62	31.09	31.20	31.36	31.30	31.52	31.70	31.96	32.34	32.50	32.59
July 6, 1972	T°C	6.43	5.81	5.04	4.87	4.74	4.70	4.34	3.82	3.73	1.99	2.75	3.42
	S‰	31.09	31.06	31.39	31.47	31.60	31.77	31.94	31.95	32.05	32.13	32.49	32.67
July10,1974	T°C	12.44	11.57	9.90	8.97	8.65	8.07	6.70	4.19	5.04	4.10	4.57	4.63
	S‰	28.53	30.08	30.83	31.13	31.23	31.44	31.67	31.76	32.13	32.41	32.59	32.65
July11,1978	T°C	12.05	10.96	10.11	9.72	9.22	8.38	6.82	6.27	6.16	5.28	4.97	4.83
	S‰	25.96	29.47	30.04	30.51	30.78	31.03	31.47	31.95	32.10	32.71	33.02	33.25

Table 21. Continued.

Date	Item	Depth (Meters)											
		0	5	10	15	20	30	50	75	100	150	200	250
July16,1982	T°C	11.66	11.29	9.77	8.92	8.48	8.04	6.90	5.41	5.53	5.33	5.39	5.44
	S‰	28.02	28.67	30.37	30.84	31.14	31.38	31.74	31.93	32.19	32.82	33.28	33.43
July20,1971	T°C	12.16		10.80		9.11	8.98	6.36	5.11	4.19	4.93	4.58	
	S‰	24.67		30.38		30.53	31.08	31.36	31.88	32.13	32.58	32.72	
July22,1976	T°C	12.65	12.38	11.54	10.99	10.97	9.72	6.96	5.28	5.10	4.82	5.08	5.13
	S‰	26.49	28.63	29.81	30.35	30.55	30.85	31.41	31.78	32.04	32.44	32.78	32.84
July25,1981	T°C	14.18	13.20	12.33	11.95	11.21	9.94	7.35	6.07	6.39	5.98	5.79	5.77
	S‰	15.35	27.57	29.02	29.51	30.25	30.70	31.38	31.82	32.19	32.54	32.77	32.81
July27,1979	T°C	13.72	13.21	12.30	11.95	11.73	11.32	7.54	5.87	5.58	5.14	5.25	5.28
	S‰	25.97	28.03	28.87	29.39	29.92	30.29	31.68	32.09	32.20	32.70	33.01	33.15
July31,1978	T°C	13.80	11.58	10.05	9.90	9.58	9.73	7.51	6.42	6.12	5.16	4.89	4.82
	S‰	26.47	29.00	29.98	30.33	30.52	31.18	31.40	31.90	32.11	32.86	33.19	33.32
Aug.16,1977	T°C	12.70	12.76	12.62	12.48	12.42	12.20	9.20	6.42	6.18	5.59	5.38	5.29
	S‰	26.76	27.18	27.71	28.63	28.98	29.61	30.99	31.99	32.37	32.95	33.16	33.29
Sep.10,1973	T°C	10.45		11.15		10.48	10.07	10.10	8.90	6.64	5.12	4.97	5.02
	S‰	23.85		29.51		30.59	31.19	31.50	31.67	31.84	32.28	32.91	33.21
Sep.11,1979	T°C	13.70	13.59	13.47	13.77	13.17	11.52	8.40	6.09	5.78	5.52	5.19	5.30
	S‰	26.20	27.26	27.52	28.56	29.01	30.41	31.40	32.11	32.22	32.56	32.96	33.12

Table 21. Continued.

Date	Item	Depth (Meters)											
		0	5	10	15	20	30	50	75	100	150	200	250
Sep.14,1971	T°C	10.65		10.90		10.94	10.91	9.80	6.81	5.53	5.02	4.92	4.93
	S‰	25.35		27.03		28.43	30.00	31.12	31.75	32.03	32.43	33.05	33.11
Sep.14,1975	T°C	11.08	11.08	11.08	11.08	11.08	10.35	8.39	6.08	6.04	4.97	4.89	
	S‰	29.81	29.81	29.81	29.81	29.81	31.06	31.67	31.90	32.23	32.85	33.20	
Sep.15,1976	T°C	11.30	11.52	11.61	11.84	11.89	11.98	10.84	8.37	6.82	5.51	4.99	5.08
	S‰	26.34	27.34	27.52	27.93	28.09	29.32	30.92	31.21	31.85	32.22	32.72	32.84
Sep.24,1978	T°C	10.85	10.77	10.87	11.46	11.54	11.60	11.19	8.14	6.84	5.47	5.10	5.01
	S‰	25.80	26.22	26.57	27.94	28.52	29.43	30.60	31.69	32.10	32.71	33.13	33.22
Oct.9,1973	T°C	8.32	8.34	8.43	8.99	9.38	9.82	9.72	7.88	6.74	5.05	5.02	5.01
	S‰	26.70	26.70	26.77	27.39	28.72	30.17	31.32	31.60	32.07	32.78	33.20	33.31
Oct.25,1972	T°C	7.58	7.59	7.59	7.60	7.60	7.78	8.48	7.91	6.37	4.41	4.57	4.73
	S‰	29.13	29.19	29.21	29.22	29.23	29.64	31.24	32.29	32.61	33.45	33.78	34.07
Oct.26,1971	T°C	7.11	7.18	7.32	7.52	7.63	7.90	9.31	9.03	8.30	5.56	5.07	4.96
	S‰	29.51	29.64	29.76	29.89	29.95	30.55	31.58	32.43	32.52	32.96	33.59	33.74
Nov.4,1975	T°C	7.08	7.08	7.07	7.08	7.07	7.14	7.49	7.99	7.63	6.14	5.34	
	S‰	30.11	30.14	30.13	30.14	30.14	30.17	30.50	31.30	31.93	32.35	32.78	
Nov.5,1976	T°C	7.56	7.57	7.57	7.57	7.59	7.68	8.40	9.27	8.58	8.27	5.65	5.29
	S‰	29.55	29.55	29.55	29.55	29.55	29.68	30.05	31.22	31.39	31.87	32.32	32.76

Table 21. Continued.

Date	Item	Depth (Meters)											
		0	5	10	15	20	30	50	75	100	150	200	250
Nov.12,1980	T°C	7.67	7.67	7.70	7.74	7.79	7.84	7.92	8.10	8.69	7.99	6.12	5.74
	S‰	29.56	29.56	29.60	29.67	29.80	29.95	30.10	30.32	31.39	32.06	32.83	33.08
Nov.12,1981	T°C	7.39	7.29	7.42	7.52	7.61	7.95	8.66	8.79	8.80	7.66	6.62	5.82
	S‰	29.06	29.06	29.09	29.16	29.20	29.47	30.20	31.00	31.37	32.17	32.54	33.02
Nov.16,1977	T°C	6.56	6.56	6.56	6.59	6.59	6.59	7.37	8.99	8.53	7.72	6.67	6.13
	S‰	29.63	29.62	29.63	29.64	29.64	29.64	30.35	31.35	31.80	32.25	32.53	32.74
Nov.17,1977	T°C	6.46	6.46	6.48	6.49	6.49	6.50	8.74	7.79	8.50	7.78	6.50	5.64
	S‰	29.80	29.82	29.79	29.80	29.80	29.83	30.83	31.11	31.79	32.22	32.61	33.03
Nov.18,1974	T°C	6.62	6.60	6.61	6.64	6.64	6.69	7.79	7.95	8.29	7.28	5.57	5.20
	S‰	29.41	29.39	29.40	29.39	29.41	29.42	30.12	31.26	31.65	31.88	32.56	33.01
Nov.21,1981	T°C	6.65	6.68	6.69	6.70	6.74	6.93	8.81	8.92	8.51	6.93	6.25	5.97
	S‰	29.37	29.39	29.39	29.40	29.42	29.61	30.93	31.48	31.90	32.56	32.89	32.97
Dec.8,1976	T°C	5.59	5.60	5.61	5.63	5.65	5.95	6.62	7.38	8.01	7.09	6.54	6.28
	S‰	28.95	28.95	28.96	28.97	28.98	29.94	29.74	30.57	31.46	32.21	32.65	32.61
Dec.14,1973	T°C	4.80		4.82		4.83	4.83	4.90	5.69	5.95	6.15	5.45	5.40
	S‰	31.03		31.04		31.04	31.04	31.06	31.38	31.72	32.14	33.13	33.25
Dec.15,1970	T°C	4.86		4.87		4.87	5.07	5.11	5.13	5.14	5.21	5.50	6.12
	S‰	31.08		31.08		31.09	31.19	31.20	31.22	31.25	31.52	31.61	32.23

Table 22. Frequency distribution (%) of maturing oocytes of Pandalus borealis offered different thermal regimes. RB=Resurrection Bay

Temperature (°C)	Date	Cell Type									
		Oogonia		Primary Oocytes		Secondary Oocytes		Yolk-bearing Oocytes		Mature Ova	
		1980	1981	1980	1981	1980	1981	1980	1981	1980	1981
3	January	59	83	25	15	14	0	0	0	0	0
	February	12	41	62	49	25	9	0	0	0	0
	March	4	10	40	47	55	42	0	0	0	0
	April	4	7	20	27	70	61	5	4	0	0
	May	4	5	15	20	69	66	12	9	0	0
	June	3	6	3	5	52	49	42	40	0	0
	July	1	5	3	4	30	27	65	61	0	2
	August	1	3	5	3	8	10	74	68	11	15
	September	2	4	4	5	8	10	50	38	35	42
	October	2	2	3	1	9	6	25	20	60	70
	November	1	1	3	2	9	6	2	4	83	85
	December	91	96	5	2	2	0	0	0	0	0
6	January	19	16	62	59	18	24	0	0	0	0
	February	4	9	49	39	46	51	0	0	0	0
	March	2	6	7	11	50	62	40	20	0	0
	April	2	6	5	9	33	28	60	57	0	0
	May	2	5	4	7	29	25	65	63	0	0
	June	2	5	1	6	6	4	91	85	0	0
	July	2	4	1	4	2	2	80	80	15	10
	August	1	3	1	3	1	1	37	47	59	45
	September	1	2	1	2	0	1	16	22	81	72
	October	1	1	0	2	0	0	0	0	97	95

Table 22. Continued.

Temperature (°C)	Date	Cell Type									
		Oogonia		Primary Oocytes		Secondary Oocytes		Yolk-bearing Oocytes		Mature Ova	
		1980	1981	1980	1981	1980	1981	1980	1981	1980	1981
	November	92	91	5	5	1	2	0	0	0	0
	December	76	69	20	26	2	3	0	0	0	0
9	January	84	80	10	13	4	5	0	0	0	0
	February	65	67	29	25	4	6	0	0	0	0
	March	18	24	63	53	18	22	0	0	0	0
	April	17	15	27	25	55	59	0	0	0	0
	May	13	14	15	26	68	54	4	6	0	0
	June	13	10	10	12	63	58	14	20	0	0
	July	13	12	4	11	33	19	50	58	0	0
	August	13	10	3	6	21	17	59	60	4	7
	September	12	9	3	6	21	5	59	70	4	10
	October	12	7	3	4	8	4	46	40	30	42
	November	12	9	3	3	8	7	1	5	75	75
	December	91	91	3	7	4	0	0	0	0	0
Resurrection Bay	February	7	-	55	-	37	-	0	-	0	-
	March	-	5	-	6	-	61	-	27	-	0
	May	5	-	7	-	30	-	58	-	0	-
	August	-	2	-	1	-	1	-	34	-	0
	September	3	-	3	-	2	-	16	-	75	-
	October	2	1	1	1	0	0	0	1	95	95
	November	-	90	-	6	-	2	-	0	-	0

Table 23. Ovarian development of Pandalus borealis in relation to temperature. A=No development visible under the carapace; B=<25%; C=25-50%; D=50-75%; E=>75% of the carapace length; F=ovigerous.

Temperature (°C)	Date	Stage of Ovarian Development Under the Carapace					
		A	B	C	D	E	F
3	July 2	92	2	0	0	0	0
	July 9	98	2	0	0	0	0
	July 16	92	5	3	0	0	0
	July 23	88	9	3	0	0	0
	August 4	80	17	3	0	0	0
	August 11	80	17	3	0	0	0
	August 18	80	17	3	0	0	0
	September 1	77	15	6	2	0	0
	September 11	65	15	13	5	2	0
	September 26	51	11	18	7	13	0
	October 4	10	14	16	10	45	5
	October 25	9	6	9	9	44	25
	November 8	9	4	1	3	15	68
	November 22	9	4	1	3	8	75
	December 6	9	3	1	1	1	85
6	July 2	80	10	5	5	0	0
	July 9	50	20	16	10	4	0
	July 16	40	34	10	12	4	0
	July 23	38	35	11	12	4	0
	August 4	31	30	16	12	11	0
	August 11	23	20	20	17	20	0
	August 18	13	7	19	35	21	5
	September 1	11	10	19	34	12	14
	September 11	10	12	12	10	25	31
	September 26	4	1	2	5	13	75
	October 4	2	1	0	0	0	97
9	July 2	100	0	0	0	0	0
	July 9	100	0	0	0	0	0
	July 16	97	3	0	0	0	0
	July 23	90	10	0	0	0	0
	August 4	88	10	2	0	0	0
	August 11	88	10	2	0	0	0
	August 18	78	10	12	0	0	0
	September 1	70	15	15	0	0	0
	September 11	63	11	5	4	17	0
	September 26	41	10	15	3	21	0
	October 4	33	5	5	5	48	4
	October 25	33	5	5	2	40	15

Table 23. Continued.

Temperature (°C)	Date	Stage of Ovarian Development Under the Carapace					
		A	B	C	D	E	F
	November 8	20	1	1	2	36	40
	November 22	20	1	1	2	22	54
	November 29	20	1	1	2	16	60
	December 7	20	1	1	2	1	75

Table 24. Comparison of spawning intensity in Pandalus borealis exposed to different thermal regimes during the 1980 and 1981 spawning seasons.

		Percent Spawned			Percent Spawned	
T°C	Dates	Weekly	Cumulative	Dates	Weekly	Cumulative
3	10-4-80	5.0		10-5-81	6.2	
	10-11-80	7.5	12.5	10-12-81	6.2	12.4
	10-18-80	2.5	15.0	10-19-81	3.7	16.1
	10-25-80	10.0	25.0	10-26-81	11.3	27.4
	11-2-80	32.5	57.5	11-3-81	33.8	61.2
	11-9-80	11.3	68.8	11-10-81	10.0	71.2
	11-16-80	3.7	72.5	11-17-81	2.5	73.7
	11-22-80	2.5	75.0	11-24-81	1.3	75.0
	11-29-80	3.7	78.7	11-30-81	2.5	77.5
	12-6-80	6.2	84.9	12-7-81	7.5	85.0
6	8-20-80	6.3		8-18-81	6.3	
	8-27-80	3.7	10.0	8-25-81	5.0	11.3
	9-1-80	3.7	13.7	9-1-81	2.5	13.8
	9-8-80	7.5	21.2	9-8-81	6.3	20.1
	9-15-80	11.3	32.5	9-15-81	10.0	30.1
	9-22-80	31.5	63.8	9-22-81	30.0	60.1
	9-29-80	18.8	82.6	9-29-81	20.0	80.1
	10-4-80	13.8	96.6	10-5-81	15.0	95.1
9	10-5-80	3.7		10-7-81	6.3	
	10-12-80	6.3	10.0	10-14-81	5.0	11.3
	10-19-80	2.5	12.5	10-22-81	1.3	12.6
	10-26-80	2.5	15.0	10-29-81	2.5	15.1
	11-3-80	11.3	26.3	11-6-81	15.0	30.1
	11-10-80	15.0	41.3	11-13-81	13.8	43.9
	11-17-80	11.3	52.6	11-20-81	13.8	57.7
	11-24-80	2.5	55.1	11-27-81	1.3	59.0
	11-31-80	8.7	63.8	12-4-81	6.3	65.3
	12-7-80	11.3	75.1	12-11-81	10.0	75.2

Table 25. Comparison of spawning activity in different size classes of Pandalus borealis exposed to different temperatures prior to the 1981 spawning season.

T°C	Size (mm CL)	No. of Shrimp	% Spawned	Julian Day	Mean Spawning Time	Duration Spawning Period (Days)
3	18	10	80	314	November 10	58(October 8-December 5)
	19	10	90	307	November 3	61(October 5-December 5)
	20	10	80	304	October 30	60(October 5-December 4)
	21	10	80	305	November 1	61(October 5-December 5)
	22	10	90	302	October 29	64(September 28-November 30)
	23	10	80	306	October 31	63(September 30-November 30)
	24	10	90	295	October 22	59(October 7-December 5)
	25	10	80	298	October 25	58(October 10-December 7)
			$\bar{X}$ 85	303.6 ± 5.7		$\bar{X}$ 60.5 ± 2.2
6	18	10	100	283	September 20	48(August 19-October 5)
	19	10	90	281	September 18	50(August 15-October 3)
	20	10	90	269	September 16	46(August 18-October 4)
	21	10	90	259	September 16	46(August 18-October 4)
	22	10	100	253	September 10	49(August 14-October 2)
	23	10	90	254	September 11	47(August 20-October 5)
	24	10	100	260	September 17	45(August 21-October 4)
	25	10	100	258	September 15	47(August 18-October 4)
			$\bar{X}$ 95	218.4 ± 3.4		$\bar{X}$ 47.1 ± 1.7
9	18	10	70	320	November 16	68(October 4-December 11)
	19	10	70	314	November 10	65(October 5-December 9)
	20	10	80	305	November 1	66(October 4-December 9)
	21	10	80	311	November 7	58(October 14-December 11)
	22	10	80	314	November 10	58(October 13-December 10)

Table 25. Continued.

T°C	Size (mm CL)	No. of Shrimp	% Spawned	Julian Day	Mean Spawning Time	Duration Spawning Period (Days)
	23	10	70	316	November 12	59(October 12-December 10)
	24	10	80	312	November 8	62(October 5-December 6)
	25	10	70	315	November 11	61(October 7-December 7)
			$\bar{X}$ 75	313.4 ± 4.3		$\bar{X}$ 62.1 ± 3.8

Table 26. Mean diamters (mm) and standard deviations (± SD) for all oocytes measured at each sampling period. Each value represents the mean of 500 measurements.

Date	Mean Exposure Temperature °C		
	3	6	9
September	0.84±0.34	0.93±0.13	0.75±0.51
October	0.97±0.27	0.98±0.11	0.81±0.67
November	0.95±0.15	0.15±0.08	0.94±0.72
December	0.09±0.17	0.29±0.34	0.06±0.03
January	0.25±0.19	0.37±0.22	0.18±0.09
February	0.33±0.26	0.44±0.20	0.21±0.18
March	0.52±0.21	0.62±0.41	0.27±0.20
April	0.57±0.36	0.69±0.36	0.41±0.32
May	0.66±0.30	0.70±0.26	0.52±0.23
June	0.72±0.19	0.75±0.09	0.56±0.11
July	0.73±0.12	0.84±0.16	0.68±0.17
August	0.79±0.17	0.90±0.21	0.72±0.10

Table 27. Relation between female size and clutch size in Pandalus borealis as a function of temperature and incubation period. Each value represents the mean of a minimum of 30 observations made in 1980 and 1981. RB=Resurrection Bay.

Temperature (°C)	Female Size (CL mm)	Mid-Point $\bar{X}$ ± SD	Mid-Point Range	End-Point $\bar{X}$ ± SD	End-Point Range
3	18	898±112	686-1110	864±103	640-1087
	19	1179±152	927-1436	1141± 91	850-1332
	20	1287±156	1031-1543	1226± 87	964-1388
	21	1446±187	1139-1763	1417± 73	1044-1710
	22	1522±112	1270-1694	1429±101	1178-1620
	23	1554± 94	1360-1748	1507±141	1266-1708
	24	2041±143	1798-2284	1972±109	1703-2211
	25	2254±160	1994-2414	2194± 82	1913-2391
6	18	931±140	641-1106	926± 87	609-1082
	19	1136±131	920-1290	1133± 63	827-1246
	20	1272±165	1050-1480	1266± 77	992-1359
	21	1532±167	1295-1740	1527± 95	1272-1627
	22	1626±182	1392-1841	1624± 56	1322-1802
	23	1748±141	1536-1962	1746± 81	1502-1942
	24	2016±130	1789-2252	2006± 76	1918-2208
	25	2258±121	2155-2502	2251± 69	2192-2489
9	18	603±180	420- 765	602±129	401- 735
	19	834±144	594-1002	831±108	523- 979
	20	949±152	721-1169	947±132	756-1141
	21	1193±189	903-1411	1191±149	850-1390
	22	1325±162	1114-1520	1324±141	1021-1502
	23	1537±154	1343-1702	1534±112	1315-1680
	24	1786±129	1607-1962	1784± 82	1589-1926
	25	1928±172	1711-2154	1926± 94	1806-2114
RB	18			654± 90	504- 820
	19			853±105	695-1009
	20			807±120	612- 951
	21			908±132	722-1089
	22			967±135	789-1202
	23			1045±146	806-1313
	24			1292±150	1098-1630
	25			1296±112	1115-1488

Table 28. Time (days) to hatching of Pandalus borealis eggs in relation to temperature and female size. Each value is the mean of 30 observations from 1979-1982.

Carapace Length mm	N	3°C		N	6°C		N	9°C	
		Mean	Range		Mean	Range		Mean	Range
18	30	185	170-233	30	114	109-120	30	104	96-124
19	30	183	172-225	30	116	111-127	30	105	100-125
20	30	184	165-234	30	115	102-120	30	98	95-130
21	30	184	180-240	30	115	110-125	30	110	102-124
22	30	182	175-238	30	118	108-130	30	107	107-137
23	30	183	167-227	30	114	107-120	30	104	97-123
24	30	182	173-238	30	117	105-125	30	103	95-123
25	30	181	179-242	30	114	103-120	30	106	90-120
		$\bar{X}$ 183 ± 1.31			$\bar{X}$ 115 ± 1.51			$\bar{X}$ 105 ± 3.46	

Table 29. Relation of Pandalus borealis larval size to incubation temperature at mean hatching time. Each value represents the mean of 20 observations.

Carapace Length mm	3°C		6°C		9°C	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
18	1.56 ± 0.07	1.50-1.60	1.41 ± 0.06	1.32-1.45	1.12 ± 0.06	0.96-1.14
19	1.47 ± 0.05	1.45-1.52	1.37 ± 0.04	1.32-1.40	0.99 ± 0.05	0.92-1.11
20	1.41 ± 0.04	1.38-1.45	1.42 ± 0.05	1.37-1.45	1.13 ± 0.07	0.98-1.14
21	1.51 ± 0.05	1.45-1.55	1.29 ± 0.04	1.16-1.35	1.00 ± 0.06	0.96-1.12
22	1.53 ± 0.03	1.47-1.56	1.39 ± 0.06	1.32-1.45	1.11 ± 0.05	0.93-1.13
23	1.42 ± 0.04	1.37-1.47	1.47 ± 0.04	1.42-1.51	1.12 ± 0.06	0.96-1.14
24	1.49 ± 0.06	1.42-1.55	1.51 ± 0.06	1.45-1.55	1.11 ± 0.05	0.98-1.13
25	1.52 ± 0.05	1.45-1.55	1.45 ± 0.05	1.42-1.51	1.13 ± 0.07	0.97-1.14
$\bar{X}$	1.49		1.41	1.09		

Table 30. Sea surface temperature off Kodiak Island, Gulf of Alaska. Data from Niebauer, 1980.

Year	March mean °C	April mean °C
1963	3.0	2.3
1964	3.3	3.8
1965	3.2	3.6
1966	4.4	3.5
1967	4.0	4.3
1968	3.4	4.2
1969	3.3	4.2
1970	5.4	5.2
1971	3.2	3.5
1972	3.0	3.5
1973	3.8	4.3
1974	3.5	4.1
1975	2.0	0.8
1976	4.1	4.0
1977	4.9	5.1
1978	3.9	5.0
1979	3.9	5.1

Table 31. Surface and bottom temperatures of bays around Kodiak Island, Alaska. *Alaska Department of Fish and Game; **National Marine Fisheries Service

Bay	Date	Temperature (°C) Surface	Temperature (°C) Bottom	Depth (M)
Alitak	1-11-80	2.2*	2.7*	61
	1-11-80	2.6*	2.6*	54
	Aug-Sept.			
	1978-80	11.0-12.4*	2.8-9.6*	86-04
	Dec-March			
	1978-80	2.2-6.1**	2.6-5.6**	86-104
	May-July			
	1978-80		2.0-3.9**	86-104
Kalsin	8-16-82	11.7**	-	75
	8-18-82	11.7**	9.2**	78
Kiliuda	Aug-Sept.			
	1978-80	10.7-12.0*	4.8-7.9*	86-104
	Dec-March			
	1978-80	3.3-3.5**	3.4-5.9**	86-104
	May-July			
	1978-80		4.5-4.9**	86-104
Pavlof	8-20-82	11.3**	--	50
		10.8	--	48
		11.3	--	68
		11.1	--	54
		11.1	3.7	54
		10.4	3.4	55
		10.3	3.8	61
		10.5	--	58
		10.3	--	64
		10.3	--	58
		10.3	--	55
		10.8	--	41
Twoheaded	1-12-80	3.7*	3.7*	130
	1-12-80	3.6	3.7	140
	1-13-80	4.1	4.1	140
	Aug-Sept.			
	1978-80	11.2*	6.3*	86-104
	Dec-March			
	1978-80	2.8-4.8**	3.7-6.0**	86-104

Table 31. Continued.

Bay	Date	Temperature (°C) Surface	Temperature (°C) Bottom	Depth (M)
Ugak	1-16-80	2.8*	2.8*	140
	8-19-82	11.7**	--	85
	Aug-Sept. 1978-80	10.9-11.2*	7.7-8.1*	86-104
	Dec-March 1978-80	2.8-5.7**	2.8-6.0*	86-104
	May-July		4.7**	86-104

Table 32. Summary of temperature effects on Pandalus borealis larvae.

Larval Processes	Temperature °C		
	3	6	9
Survival	Low	Medium	High
Growth	Same	Same	Same
Instars Required	High	Medium	Low
Feeding Rates	Low	Medium	High
Resistance to Starvation	Low	Medium	High

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GLOSSARY

GLOSSARY

amino acid - an organic acid used in constructing protein molecules

atretic oocytes - regression or resorption of yolk-bearing oocytes

benthic - pertaining to the sea bottom and the organisms that inhabit the bottom

bloom - a dense concentration of phytoplankton which occurs in response to optimum growth conditions

brachyuran - a suborder of Decapoda comprising crustaceans with the abdomen greatly reduced and more or less folded against the ventral surface of the thorax and including the typical crabs

carapace - the dorsal section of the exoskeleton of some crustaceans, enlarged to shield the cephalothoracic segments of the body

chorionic membrane - outer membrane surrounding an egg cell

critical period - refers to the transition from yolked larva stages to those requiring the provision of the proper kind and amount of food

Decapoda - order of Malacostracan Crustacea which include the crayfish, crab, lobster, shrimp; thoracic appendages mostly uniramous; last five thoracic segments with "walking legs"

diatoms (Bacillariophyceae) - a group of mainly unicellular chrysophyte algae forming a principal component of marine and freshwater plankton; they have silica cell walls (frustules) composed of two valves ornamented with perforations, which are arranged differently in each species; they are typically pill-box shaped (centric) or coffin-shaped (pennate); diatoms reproduce asexually by binary fission producing successively smaller generations until size is restored through sexual reproduction by auxospores

digestive gland (hepatopancreas) - digestive or storage gland in shrimp; also known as gastrohepatic gland

dinoflagellates (Dinophyceae) - a group of planktonic unicellular algae forming part of the Pyrrophyta; most are biflagellate with one flagellum encircling the cell, the other trailing backwards (sometimes both are apical); often contain fucoxanthin; marine forms are typically naked protoplasts but freshwater forms normally possess a cell wall, which may have spiny processes or thickened plates (as flotation devices); sexual reproduction is rare and usually oogamous

ecdysis (molting) - the periodic shedding of the exoskeleton of arthropods to permit an increase in size and/or change of form

eurythermal - able to withstand a wide range of temperatures; cf. stenothermal

exoskeleton - an external skeleton, particularly characteristic of arthropods

eye placode - localized ectodermal thickening, forerunner of the larval eye

eyepiece micrometer - linear scale mounted in element of microscope near eye, enabling measurement of small structures

fecundity - number of eggs, sperm or young produced by an animal in one breeding season

follicle cells - peritoneal cells which surround the ova and pass on food from a special blood supply

hermaphrodite - an organism capable of functioning both as a male and a female during its lifetime

homeostasis - tendency of living organisms to maintain a steady state in their internal environmental conditions, including body temperature, blood sugar level and metabolic state

instar - generic term for larval stages

larvae - generic term for early stages of shrimp after hatching from the egg, morphologically distinct from the adult

lipid - a class of organic compounds, includes fats, oils, waxes and steroids

meiosis - a process of cellular division which reduces the chromosome number by one-half

megalopa - transitional stage between zoea and juvenile; stage immediately preceeding metamorphosis; rostrum with 13-15 dorsal teeth; flagellum of antenna six times length of antennal scale; lateral margins of telson converge posteriorly but widen slightly at junction with posterior margin, typically four spines on each lateral margin, 3 + 3 stout spines on posterior margin

meroplankton - planktonic organisms that spend only part of their life cycles in the plankton

metamorphosis - the stage in the life history of some animals during which the larval form undergoes abrupt transformation to the adult form

mitosis - a process of cell division resulting in two daughter cells genetically identical to their parent cell

multiparous - having produced more than one previous brood

Natantia - a suborder of Decapoda comprising crustaceans (such as shrimp, prawns and related forms) that have the rostrum usually long, the first antenna with a stylocerite, the second antennal scale larger, the abdomen well developed, somewhat compressed laterally, and frequently flexed ventrally

nucleolus - one or more small, dense, more or less spherical bodies in the nucleus of non-dividing cells; apparently produced by chromosomes and contain ribose

nucleoprotein; quite distinct from the karyosomones

ontogency - the development of an individual during its lifetime from fertilized egg to the adult

oocyte - reproductive cell in the ovary of an animal that undergoes meiosis to form an ovum

oogenesis - series of cell divisions and chromosome and cytoplasmic changes involved in the production of functional ova, beginning with undifferentiated germinal epithelium, passing through oogonial cells, and especially the changes of primary oocytes through secondary oocytes to a mature egg or ovum

oogonium - a cell in the ovary of an animal that undergoes a period of multiplication and growth to give rise to an oocyte

optimal/optimum - those conditions most favorable for growth and reproduction of an organism or the maintenance of a system

ovigerous - egg-bearing; pertaining to the condition of, or a female, carrying external fertilized eggs

ovum - mature but unfertilized egg

Pandalidae - distinguished from all other families of shrimp in its arrangement of pointed and pincer-tipped legs. Each leg of the first, third, fourth and fifth pairs has a sharply pointed tip; each leg of the second pair has a small pincer at the tip

pelagic - pertaining to the waters of the ocean and the organisms which inhabit the water column

Penaeidae - abdominal pleurae of the second segment of this family of shrimp do not overlap those of the first; first three pairs of legs chelate; the only decapod group to retain a free swimming naupliar stage

planktonic - free floating in the water column

planktotrophic - larvae that feed in the plankton

pleopod - paired abdominal appendages in crustaceans of the first five abdominal somites (rarely six) in Malacostraca, primarily used for swimming

poikilotherm - an organism whose body temperature varies with and is largely controlled by environmental temperatures

postlarvae - generic term for early juvenile stages immediately following metamorphosis

primiparous - bearing young for the first time

protandrous hermaphrodite - occurrence of male phase prior to the female phase in the same individual

QO_2 - rate of oxygen consumption

spawning - in aquatic animals, to produce or deposit eggs or sperm

vacuole - a liquid or food-filled cavity within the cell

Van't Hoff's Law - Q_{10} Law; doubling of the rate of a chemical reaction for every ten degree C increase in temperature; not a precise generalization since as indicated by many biological processes and activities, the measured rate is usually 1.5 to 4.0

vitellogenesis - yolk formation

zoeae - an early larval form of decapod crustaceans and especially of crabs and anomurans that commonly precedes the megalops and that is distinguished by the relatively large cephalothorax commonly bearing three or four long spines, the conspicuous eyes, the relatively large and fringed antennae and mouthparts used for swimming, the rudimentary thoracic appendages, and the long slender abdomen having small or no swimmerets

stage I:eyes sessile; rostrum without teeth and about one-third length of carapace; 3 pairs of pereopods; no pleopods; antenna shorter than scale, unsegmented and tipped with one spine; uropods enclosed, telson not segmented from sixth abdominal somite with 7 = 7 posterior setae

stage II:eyes stalked; rostrum still without teeth; five pairs of pereopods; pleopods present as distinct buds; antenna still shorter than scale but segmented and tipped with 3 spines; uropods still enclosed, telson distinctly jointed from sixth abdominal somite with 8 + 8 posterior setae, anal spine present but minute

stage III:rostrum with one or two teeth at base; pleopods bilobed, unsegmented and without setae; flagellum of antenna eight-segmented, about equal in length to scale; uropods free but endopodite not fully developed, about one-third length of exopodite

stage IV:rostrum bears 4-8 but usually 6 dorsal teeth, no ventral teeth, tip not bifid; flagellum of antenna 15-segmented, 1.5-2 times length of scale; endopodite of uropod about two-thirds length of exopodite, lateral margins of telson nearly parallel but slightly divergent posteriorly and bear 2 spines each; posterior margin still slightly emarginate bearing 6 + 6 spines

stage V:rostrum with 9-12 dorsal teeth, bifid tip, usually 4 but sometimes 5 ventral teeth; flagellum of antenna 2-3 times the length of scale; lateral margins of telson especially parallel and bear 2 spines each, posterior margin straight bearing 6 + 6 spines